UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LES LICHENS ÉPIPHYTES DANS LA PESSIÈRE À MOUSSES DE L'OUEST DU QUÉBEC : INDICATEURS DE LA QUALITÉ ET DE LA FRAGMENTATION DES HABITATS

THÈSE PRÉSENTÉE

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AVANT-PROPOS

Cette thèse comporte quatre chapitres rédigés en anglais sous forme d'articles scientifiques, ainsi qu'une introduction et une conclusion générale rédigées en français. Pour les quatre chapitres, je suis l'instigatrice principale des projets et première auteure des articles. Pour tous ces chapitres, j'ai planifié le travail de terrain, analysé les données en laboratoire, fait les analyses statistiques et rédigé les articles. J'ai réalisé le travail de terrain des chapitres 1, 3 et 4 au cours des étés 2003 à 2006. Pour le chapitre 2, les branches ont été récoltées, selon mes directives, par Liliana Mascarúa López dans le cadre de ses travaux de maîtrise. Elle et son équipe de terrain ont donc sélectionné les sites et ils ont réalisé le travail de terrain. Liliana Mascarúa López, ayant fait le travail de terrain, et Pierre Drapeau, ayant collaboré à la rédaction de l'article, sont donc co-auteurs de ce chapitre. Pour le chapitre 4, j'ai bénéficié de l'aide de Bob Saggar pour l'installation et pour la programmation des stations météo. Bernhard Denneler s'est occupé de l'entretien de ces dernières et de la fabrication de la serre permettant de peser les lichens sous des conditions d'humidité et de température contrôlées. Les analyses de viabilité ainsi que les analyses concernant le contenu en eau des lichens ont été réalisées par Darwyn Coxson à UNBC. Suzan Stevenson m'a conseillée pour la planification de l'échantillonnage du chapitre 1 et est co-auteure du chapitre 4. Elle a développé, en collaboration avec Darwyn Coxson, la méthode utilisée dans le chapitre 4 pour étudier la croissance des lichens. Suzan Stevenson a aussi participé à la récolte des échantillons pour cette étude et à la rédaction de l'article. Mathieu Bouchard a relu toutes les versions préliminaires de ces chapitres et a participé activement au travail de terrain et à la rédaction du chapitre 4. À la fin de chaque chapitre, apparaissent les noms des diverses personnes qui ont participé au travail de terrain ou de laboratoire, qui m'ont aidée avec les analyses statistiques ou qui ont révisé l'anglais.

Au moment du dépôt de cette thèse, le chapitre 1 avait été publié en 2009 sous le titre de «**Factors controlling epiphytic lichen biomass during postfire succession in black spruce boreal forests** » dans *La revue canadienne de recherche forestière* 39 : 2168-2179.

Le deuxième chapitre intitulé « **Edge effects on epiphytic lichens in remnant stands of managed landscapes in the eastern boreal forest of Canada** » avait été publié en 2008 dans *Forest Ecology and Management* 255 : 1461-1471.

Le troisième chapitre n'était pas soumis et le quatrième chapitre était sur le point d'être soumis dans la revue *Ecological Applications* sous le titre « **Do canopies opened by partial cutting provide growth conditions similar to old-growth forests for two epiphytic lichens in black spruce boreal forests?** »

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La structure des communautés de lichens épiphytes de la forêt boréale demeure peu décrite, particulièrement dans les forêts d'épinette noire de l'est de l'Amérique du Nord. Il est important de mieux décrire ces communautés et de mieux comprendre les facteurs qui déterminent l'abondance des différentes espèces ou groupes d'espèces de lichens épiphytes. Ces connaissances seront utiles pour formuler des recommandations d'aménagement, dans l'optique où il est de plus en plus reconnu que les pratiques d'aménagement forestier ne doivent pas mettre en péril le maintien de la biodiversité et des processus écosystémiques.

Le premier chapitre contient une évaluation de l'influence du temps depuis le dernier feu, de la structure du peuplement, de la taille et de l'âge des arbres ainsi que la hauteur des branches sur la biomasse de lichens épiphytes dans la forêt boréale de l'Ouest du Québec. Nous avons échantillonné 12 sites appartenant à quatre stades de développement (de 50 à >200 ans). Nous avons estimé la biomasse de trois groupes de lichens épiphytes (*Bryoria*, *Evernia* et *Usnea*) sur 12 arbres dans chaque site. Nos résultats ont montré que la biomasse de *Bryoria* et d'*Usnea* était plus élevée dans les stades intermédiaires de développement (entre 101 et 200 ans) comparativement aux plus jeunes (50–100 ans) et plus vieux stades (>200 ans). La biomasse des trois groupes était supérieure sur les arbres de plus gros diamètres (>16 cm) comparativement aux plus petits arbres (<16 cm). Ces résultats indiquent que la protection des peuplements après feu âgés de 101 à 200 ans devrait être priorisée afin de maintenir le rôle fonctionnel des lichens épiphytes dans les paysages aménagés.

Le second chapitre vise à comparer les communautés de lichens épiphytes dans différents types de forêts résiduelles laissées après coupe et de comparer les effets de lisière entre des forêts résiduelles linéaires étroites et de plus grandes forêts. Nous avons comparé la biomasse totale de différents groupes de lichens épiphytes (*Bryoria* spp., *Usnea* spp., and *Evernia mesomorpha*) dans quatre différents types de forêts : séparateurs de coupe linéaires, bandes riveraines, grands blocs de forêts résiduelles et forêts d'intérieur. Nous avons aussi examiné si les effets de lisières sur la biomasse lichénique étaient présents dans deux types de forêts résiduelles parmi les quatre, soit les séparateurs linéaires et les grands blocs de forêts résiduelles. Les résultats indiquent que la biomasse de *Bryoria* était plus élevée dans les grands blocs résiduels et dans les forêts d'intérieur par rapport aux bandes riveraines et aux séparateurs de coupe, et que la biomasse d'*Evernia* était plus élevée dans les bandes riveraines que dans les autres types de forêts. La biomasse d'*Usnea* ne variait pas selon les types de forêts. Le long des transects localisés perpendiculairement à la lisière dans les deux types de forêts résiduelles linéaires, la biomasse de *Bryoria* à 0 et 15 m à l'intérieur de la lisière était significativement plus basse qu'à 30 m. La biomasse d'*Evernia* et d'*Usnea* était significativement plus basse à la lisière de la coupe totale (0 m) comparativement aux parcelles localisées à l'intérieur (30 m). Nos résultats suggèrent que dans un paysage où seuls

des séparateurs de coupe et des bandes riveraines seraient laissés en guise de forêts résiduelles, les communautés de lichens épiphytes typiques des forêts d'intérieur pourraient ne pas se maintenir, particulièrement les biomasses élevées de *Bryoria* observées dans les forêts d'intérieur.

Le troisième chapitre porte sur la colonisation des jeunes peuplements par les lichens épiphytes, un phénomène important pour le maintien de populations viables dans les paysages forestiers affectés périodiquement par les perturbations sévères. Nous avons examiné la colonisation de différentes espèces relativement communes de lichens foliacés et fruticuleux épiphytes dans des peuplements d'épinette noire en régénération dans la forêt boréale de l'ouest du Québec. Le nombre de thalles ainsi que l'abondance des espèces ont été mesurés sur des branches prélevées sur des jeunes arbres localisés dans des coupes totales, à différentes distances de forêts matures adjacentes (de 5 m à 100 m). Nous avons échantillonné des peuplements régénérés de deux façons, soit des peuplements issus d'une régénération naturelle qui s'est établie en sous-étage avant la coupe totale, et des peuplements régénérés par plantation suite à la coupe. Les lichens ont aussi été inventoriés dans deux classes d'âge de coupes, soit des coupes âgées de 12 à 18 ans et des coupes âgées de 6 à 12 ans. Les résultats indiquent que pour les jeunes coupes, le nombre de thalles et l'abondance par branche étaient supérieurs dans les peuplements issus de régénération naturelle pour la plupart des espèces de lichens épiphytes, alors que cette différence entre les deux types de régénération s'estompait dans les peuplements plus âgés. La distance par rapport au peuplement adjacent exerçait peu d'influence sur l'abondance des thalles pour la plupart des espèces, sauf pour celles qui se dispersent principalement par fragments de thalles, et particulièrement *Bryoria* spp., pour lesquelles le nombre de thalles était significativement plus élevé à 5 m qu'à 100 m. Ces résultats suggèrent donc que la plupart des espèces de lichens parviennent à coloniser les microsites présents dans les peuplements en régénération, peu importe l'origine de cette régénération.

Dans le quatrième chapitre, nous examinons les taux de croissance de deux espèces de lichens épiphytes, *Bryoria nadvornikiana* et *Evernia mesomorpha*, en fonction de différents gradients d'ouverture du couvert. Les taux de croissance ont été évalués à partir de transplants installés dans deux types de peuplements, soit de vieux peuplements vierges et des vieux peuplements récemment traités par coupe partielle. Les accroissements ont été mesurés sur une période de deux ans, et plusieurs variables environnementales ont été mesurées directement sur les sites pour faciliter l'interprétation des résultats. Les résultats indiquent que malgré une variation importante dans les taux de croissance chez les deux espèces de lichens dans les différents types de peuplements, la création d'ouvertures dans le couvert dominant suite à des coupes partielles a un effet significatif et affecte négativement la croissance des deux espèces. La réponse négative est proportionnelle au degré d'ouverture dans le couvert dominant et *B. nadvornikiana*, une espèce généralement davantage associée aux couverts forestiers fermés, est significativement plus affectée qu'*E. mesomorpha*, une espèce plutôt associée aux couverts forestiers plus ouverts. Dans la discussion, nous soulignons que cette réponse négative contraste avec ce qui est généralement rapporté dans la littérature en ce qui

concerne l'effet de la création d'ouvertures sur la croissance des lichens épiphytes. En fonction de l'analyse des différents paramètres environnementaux mesurés, nous suggérons que la réduction de la durée d'hydratation dans les coupes partielles, le risque accru de la fragmentation des thalles dans les coupes partielles, le climat relativement sec qui prévaut dans cette région, ainsi qu'une année particulièrement sèche lors de la deuxième année de l'étude peuvent expliquer ces résultats. Les résultats ne remettent pas en cause le fait que les coupes partielles peuvent contribuer au maintien des populations de lichens épiphytes au niveau du paysage, surtout lorsque l'on compare cette pratique aux coupes totales qui prévalent généralement dans cette région. Ils suggèrent néanmoins que, dans notre région, les peuplements récemment traités par coupe partielle offrent des conditions de croissance inférieures à celles que l'on retrouve dans les peuplements non coupés.

Dans l'ensemble, cette thèse a permis de faire avancer significativement les connaissances sur les mécanismes déterminant la structure et la composition des communautés de lichens épiphytes en forêt boréale, en particulier en ce qui concerne la dispersion et la croissance de différentes espèces en fonction de différentes variables environnementales. Nous avons montré que la biomasse en lichens varie en fonction de la qualité et de la quantité de substrats disponibles pour la colonisation, tant à l'échelle de la branche, de l'arbre, du peuplement et du paysage. La qualité et la quantité de substrats pour les lichens sont intimement liées au temps écoulé depuis la dernière perturbation. La structure du couvert forestier influence fortement les conditions environnementales prévalant dans les forêts et ces conditions auront une influence importante sur les populations de lichens épiphytes. Les forêts d'intérieur semblent les plus propices au maintien de populations qui pourront servir de foyers pour la recolonisation des superficies perturbées récemment. Le maintien d'une proportion significative de parcelles de forêts matures (100 à 200 ans) présentant des conditions de forêt d'intérieur apparaît donc comme une mesure de précaution intéressante à adopter dans un contexte d'aménagement forestier.

Mots clés : lichens alectorioides, effets de lisière, coupes partielles, croissance, dispersion, colonisation.

INTRODUCTION GÉNÉRALE

Dans cette étude, je me suis intéressée aux communautés de lichens épiphytes dans la pessière à mousses de l'Ouest du Québec (Saucier et Robitaille, 1998), plus spécifiquement dans la pessière à mousses du nord de l'Abitibi. Cette thèse visait à acquérir des connaissances fondamentales sur l'écologie des lichens, considérant que peu d'études ont été menées dans cet écosystème. Elle visait aussi à faire en sorte que ces résultats puissent être utilisés afin d'améliorer les chances de préserver la diversité biologique dans un contexte d'aménagement forestier écosystémique. Au début de ce projet, à l'exception de l'étude de Rheault *et al.* (2003) sur les effets de lisière, les connaissances que nous avions des impacts des coupes forestières sur les lichens épiphytes provenaient de la forêt fennoscandinave et, en Amérique du Nord, de la forêt de la côte du Pacifique. Or, les recommandations formulées pour préserver la biodiversité pour certaines régions ne s'appliquent donc pas nécessairement pour d'autres. En effet, les régions mentionnées sont caractérisées par des régimes de perturbations différents de ceux qui prévalent dans le nord de l'Abitibi. Par exemple, dans la forêt boréale fennoscandinave, les feux sont souvent moins destructeurs que les feux de couronne caractéristiques de la forêt boréale canadienne (Kneeshaw *et al.*, sous presse). Dans les forêts de Colombie-Britannique, le climat est pluvieux, les feux sont plus rares, la quantité de vieilles forêts est plus importante, et ces forêts sont généralement plus structurées que celles que l'on retrouve au Québec (Coxson et Radies 2008). À ma connaissance, en forêt boréale de l'est du Canada, aucune étude n'avait porté sur certains processus importants pour les populations de lichens épiphytes, telles la colonisation et la croissance. De plus, l'importance des divers stades de développement des peuplements pour le maintien de la diversité et de l'abondance des lichens épiphytes était peu documentée (Boudreault *et al.*, 2002; Yarranton, 1972).

Dans la première partie de l'introduction, j'expliquerai le contexte général de l'étude, soit le régime de perturbations et la succession forestière caractéristiques de la région à l'étude, et le concept de fragmentation forestière. J'expliquerai aussi les approches proposées pour

aménager de façon écosystémique la pessière à mousses de l'Abitibi. Dans la seconde partie, j'insisterai sur l'utilisation des lichens épiphytes comme indicateurs de la qualité des habitats et de la fragmentation du paysage, et comment ceux-ci peuvent être utilisés dans un contexte d'aménagement écosystémique.

0.1 Régime de perturbations et succession forestière dans la pessière à mousses du nord de l'Abitibi

La dynamique forestière en forêt boréale est fortement influencée par les feux de forêt (Payette, 1992). De façon générale, ce sont les feux de couronne de grande superficie qui laissent leur empreinte sur le paysage forestier québécois; même s'ils sont moins nombreux que les feux de petite superficie, ces feux affectent une proportion beaucoup plus importante du territoire (Bergeron *et al.*, 2002).

Dans plusieurs régions de l'est du Canada, l'intervalle moyen entre deux feux successifs est suffisamment long pour qu'une portion significative du territoire soit composée de vieux peuplements de structure inéquienne et irrégulière (Bergeron *et al.*, 2001). Dans la ceinture d'argile de l'Abitibi, l'âge moyen des forêts est de près de 150 ans (Bergeron *et al.*, 2001). Dans ces peuplements, la chute d'un ou de plusieurs individus suite à des perturbations secondaires telles que le chablis, la sénescence et parfois des épidémies d'insectes (St-Denis *et al.*, 2010), permettent aussi de recruter de nouveaux individus dans la canopée.

Contrairement à ce qui est observé dans le domaine de la sapinière (Bergeron, 2000), la pessière à mousses se caractérise par une succession forestière dans laquelle il y a relativement peu de remplacement d'espèces, particulièrement lorsque la régénération après feu est assurée par l'épinette noire (Gauthier *et al.*, 2004). Il a toutefois été observé que la structure de ces peuplements change considérablement avec le temps (Harper *et al.*, 2003). Environ 100 ans après un feu, la canopée des forêts est relativement fermée, et elle s'ouvre progressivement par la suite à mesure que meurent les arbres de la cohorte qui s'était installée immédiatement après feu (Simard *et al.*, 2007). Avec le temps, des changements importants au niveau du sous-bois sont aussi observés : le recouvrement des éricacées a tendance à

augmenter, alors que les mousses hypnacées se font graduellement remplacer par les sphaignes (Boudreault *et al.*, 2002; Fenton *et al.*, 2005).

Le processus de paludification successionnelle, défini comme une accumulation de la couche organique avec le temps sur les sites avec des pentes faibles, est un phénomène particulièrement important dans la région Ouest de l'Abitibi dominée par des dépôts d'origine glacio-lacustre, majoritairement composés d'argiles et mal drainés (Boudreault *et al.*, 2002; Fenton *et al*, 2005; Simard *et al.*, 2007). Ce processus écologique confère aux vieilles forêts de cette région des caractéristiques particulières qui peuvent différer de ce que l'on retrouve dans les vieilles forêts boréales ailleurs au Québec. Ainsi, les plus vieux sites seront typiquement caractérisés par une forte épaisseur de matière organique composée majoritairement de sphaignes, une canopée relativement ouverte et une faible productivité (Simard *et al.*, 2007).

0.2 Fragmentation

La fragmentation est le processus par lequel un paysage plus ou moins homogène est divisé en petites parcelles, isolées les unes des autres par une matrice (définie ici comme étant l'espace entre les fragments) de végétation différente (Meffe et Carroll, 1994). De façon générale, les paysages fragmentés par des perturbations anthropiques sont plus homogènes tant au niveau spatial que temporel et présentent un plus faible taux de connectivité entre les habitats résiduels (Meffe et Carroll, 1994). Les trois composantes principales de la fragmentation et leurs impacts sur la biodiversité seront abordés dans les sous-sections suivantes.

0.2.1 Réduction de la taille des habitats

La réduction de la taille d'un habitat entraîne généralement une diminution de la taille des populations (Saunders *et al.*, 1991). La probabilité d'extinction stochastique due à des facteurs démographiques, environnementaux et génétiques est plus élevée dans les petites

populations (Mönkkönen, 1999). Les petites populations peuvent cependant persister pour de longues périodes de temps dans un paysage fragmenté, simplement en raison de la longévité des individus, sans toutefois être viables à long terme si la reproduction et le recrutement de nouveaux individus ne sont pas assurés (Saunders *et al.*, 1991).

0.2.2 Isolement des habitats et nature de la matrice

L'isolement des îlots forestiers peut entraver le mouvement des individus ou des diaspores entre les différents types d'habitat ou entre des habitats de même type et menacer la persistance à long terme de certaines populations. En effet, la taille démographique et génétique des populations ne sera pas accrue par des événements de colonisation externes (« effet de sauvetage ») (Brown et Kodric-Brown, 1977) et les espèces ne pourront pas augmenter leur distribution en colonisant des sites non occupés ou en recolonisant les sites après extinction en raison de barrières à la dispersion (Hanski, 1999; Johansson et Ehrlén, 2003). Ces barrières à la dispersion peuvent toutefois être atténuées si la matrice contient des attributs (p. ex., corridors et des arbres laissés sur pied) qui augmentent la connectivité entre les habitats, ou qui permettent aux espèces de persister dans la matrice. De plus, les forêts coupées pourront, éventuellement, accueillir à nouveau les espèces disparues, à mesure que les forêts se régénéreront par la succession (Johst *et al.*, 2002; Murphy et Lovett-Doust, 2004). Dans une matrice dynamique comme le sont les forêts de milieu boréal, l'échelle temporelle de la destruction et de la régénération des habitats est donc d'une grande importance pour les populations (Johst *et al.*, 2002; Laurence *et al.*, 2002).

0.2.3 Effets de lisière

La fragmentation du paysage entraîne une altération importante du microclimat dans une zone située à l'interface entre deux unités avec de forts contrastes structuraux. Parmi les changements pouvant être observés en bordure, on peut identifier l'augmentation de la radiation solaire, de la température de l'air, de la vitesse du vent et une diminution de l'humidité de l'air et du sol (Chen *et al.*, 1995; Matlack, 1993). La végétation peut être affectée de façon directe par les changements microclimatiques (p. ex., chute des arbres;

Esseen, 1994) ou de façon indirecte via des changements au niveau de la structure de la forêt (p. ex., augmentation des espèces de lumière; Harper et Macdonald, 2002). Les effets peuvent toutefois s'atténuer à mesure que la jeune forêt se régénère et que les contrastes s'atténuent (Harper *et al.*, 2005). La zone d'intérieur d'un fragment, non soumise à l'influence d'une ou de plusieurs lisières, est influencée par la taille et la forme du fragment (Saunders *et al.*, 1991). Les fragments linéaires et étroits ont proportionnellement plus de lisières que les fragments carrés ou circulaires (Saunders *et al.*, 1991). Dans certains types d'habitats résiduels très petits de forme linéaire (bandes riveraines et séparateurs de coupe), les organismes peuvent être influencés non seulement par la lisière la plus proche, mais aussi par d'autres lisières plus éloignées (Malcolm, 1994; Mascarúa López *et al.*, 2006).

0.3 Aménagement écosystémique en forêt boréale

0.3.1 Fondements et enjeux écologiques

La conservation de la biodiversité est un critère de développement durable des forêts (CCMF 1995). Selon l'approche d'aménagement écosystémique des forêts (AFE) tel que définie par Gauthier *et al.* (2008)[1], la meilleure façon de conserver la diversité biologique est de réduire les écarts entre la forêt aménagée et la forêt naturelle (Bergeron *et al.*, 2002). Pour arriver à cet objectif, on peut s'inspirer des perturbations naturelles à l'échelle régionale (Attiwill, 1994; Bergeron *et al.*, 2002) afin de recréer des paysages aménagés semblables à des paysages naturels (en termes de composition, de structure et d'agencement spatial des forêts). En effet, si les effets des coupes forestières se situent à l'intérieur de la variabilité historique du régime de perturbations (Bergeron *et al.*, 2002), les effets des coupes sur la diversité des écosystèmes, des espèces et des gènes devraient être limités puisque les écosystèmes et les espèces sont adaptés au régime de perturbations naturelles qui surviennent en forêt boréale.

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[1] «Une approche d'aménagement qui vise à maintenir des écosystèmes sains et résilients en misant sur une diminution des écarts entre les paysages naturels et ceux qui sont aménagés afin d'assurer, à long terme, le maintien des multiples fonctions de l'écosystème et, par conséquent, de conserver les bénéfices sociaux et économiques que l'on en retire».

Or, les effets des coupes se situent souvent hors de la variabilité historique du régime de perturbations (Cyr *et al.*, 2009).

L'aménagement forestier au Québec a entrepris un virage en 2005 lorsque le Ministère des Ressources Naturelles et de la Faune s'est engagé à favoriser l'application d'un AFE dans les forêts publiques du Québec pour assurer le développement durable des forêts. Les écarts significatifs existant entre les forêts naturelles et les forêts aménagées constituent donc des enjeux écologiques importants à identifier pour le maintien de la biodiversité (Jetté *et al.*, 2008).

Parmi ces enjeux, notons notamment la raréfaction des vieux peuplements et la modification de la configuration spatiale des habitats. Même pour les régions qui sont fortement affectées par les feux et même lorsque la révolution forestière est de même durée que le cycle de feu, les distributions de classes d'âge produites par les coupes totales et les feux sont différentes (Bergeron *et al.*, 2002; Jetté *et al.*, 2008). En effet, les pratiques forestières entraînent une diminution importante des vieilles forêts qui occupent naturellement une proportion importante du territoire et dont la structure est plus complexe au profit des forêts en régénération (Bergeron *et al.*, 2002; Harper *et al.*, 2002). Avec cette raréfaction des vieilles forêts et la perte concomitante d'éléments de structure particuliers qui leur sont associées (p. ex., chicots, débris ligneux, vieux arbres), certaines espèces inféodées aux vieilles forêts pourraient être menacées (Drapeau *et al.*, 2003; Gauthier *et al.*, 2004).

Les grands feux sont souvent éloignés les uns des autres (Belleau *et al.*, 2007; Perron *et al.*, 2008). À l'intérieur des zones brûlées, une forte proportion du territoire est constituée d'îlots de végétation non brûlés et partiellement brûlés (Kafka *et al.*, 2001; Bergeron *et al.*, 2002), de forme plus ou moins régulière (Bergeron *et al.*, 2002; Greene et Johnson, 2000; Kafka *et al.*, 2001; Turner et Romme, 1994) qui pourront servir de refuges, permettront de recoloniser les brûlis et augmenteront l'hétérogénéité spatiale et la connectivité entre les habitats (Leduc *et al.*, 2000). À l'opposé, à l'intérieur des immenses aires en régénération des chantiers de coupes agglomérées, seuls quelques fragments de forêts résiduelles plus ou moins isolés les uns des autres (p. ex. séparateurs de coupe, bandes riveraines, forêts improductives)

subsisteront, entraînant ainsi une raréfaction et une fragmentation des grands massifs de vieilles forêts (Bergeron *et al.*, 2002; Jetté *et al.*, 2008). À l'échelle du peuplement, les aires aménagées laissent très peu d'arbres sur pied pouvant imiter les vétérans observés dans les zones partiellement brûlées (Vaillancourt *et al.*, 2008). De plus, les contrastes entre les peuplements adjacents sont plus importants dans les paysages aménagés (p. ex., entre une vieille forêt et une zone en régénération), car les coupes ne sont pas encerclées de zones d'exploitation moins intensives imitant les zones partiellement brûlées entourant les zones préservées du feu (Harper *et al.*, 2004). La forme linéaire de la plupart des peuplements résiduels d'un paysage aménagé (séparateurs de coupe et bandes riveraines) accentue les effets de lisière, au détriment des espèces associées aux habitats d'intérieur.

0.3.2 Aménagement écosystémique dans la pessière à mousses de l'Abitibi

L'approche par cohortes a été proposée afin d'aménager de façon écosystémique la pessière à mousses de l'Ouest du Québec (Bergeron *et al.*, 2002; Gauthier *et al.*, 2004). En s'inspirant de la succession naturelle des peuplements après le passage d'un feu sévère, les peuplements ont été séparés en fonction de leur âge et de leur structure en trois cohortes, représentant les diverses phases de développement (début, milieu et fin de succession; Gauthier *et al.*, 2004). Un aménagement mixte est donc proposé afin de recréer ou maintenir les caractéristiques structurales et compositionnelles des diverses cohortes à l'échelle d'une unité d'aménagement (Gauthier *et al.*, 2004). Une proportion du territoire est donc soumise à la coupe totale et est donc principalement constituée d'aires en régénération visant à recréer les peuplements équiennes issus de feux. À l'intérieur des chantiers de coupes totales, Drapeau *et al.* (2008) proposent de maintenir des îlots de forêts résiduelles, des arbres individuels et des bouquets d'arbres dans des proportions et selon une configuration qui s'apparentent à celles observées après feu. Ils proposent également des stratégies de rétention permanente de forêts « de qualité », avec une structure diversifiée et connectées les unes aux autres, visant à assurer le maintien des fonctions écologiques des forêts, et à faciliter la recolonisation des aires de coupe et le maintien à long terme de la biodiversité. Une autre portion du territoire est traitée par coupes partielles afin (1) d'éduquer les peuplements vers des structures de

cohortes plus vieilles (coupes de succession) ou (2) de conserver la structure d'un peuplement qui est déjà à la deuxième ou à la troisième cohorte (Bouchard, 2008), et ainsi maintenir ou recréer les caractéristiques structurales propres aux peuplements anciens (Fenton *et al.*, 2008). L'utilisation de coupes partielles pour recréer la structure irrégulière des peuplements surannés et anciens dans les paysages où la composante de vieux peuplements est importante reste encore marginale. C'est dans ce contexte qu'un dispositif expérimental de coupes partielles a été mis en place en Abitibi.

À l'aide d'indicateurs forestiers, un programme de suivi environnemental a été proposé par Drapeau *et al.* (2008) pour s'assurer que les cibles fixées dans une approche d'AFE permettent effectivement de maintenir la diversité biologique dans les paysages aménagés. Selon ces auteurs, des organismes susceptibles de répondre fortement et rapidement aux changements des paysages forestiers et associés aux habitats les plus affectés par l'aménagement des forêts font de bons indicateurs. Les connaissances acquises au moyen de ces indicateurs permettront de moduler les pratiques sylvicoles afin de maintenir les conditions forestières requises pour le maintien de la diversité biologique (Drapeau *et al.*, 2008).

0.4 Les lichens épiphytes comme indicateurs de la qualité des habitats forestiers et de la fragmentation des habitats

Les lichens épiphytes sont un groupe diversifié, souvent associés aux vieilles forêts et sensibles aux modifications environnementales. Ils constituent donc un groupe d'indicateurs à privilégier pour étudier les impacts de l'aménagement forestier sur la diversité biologique.

0.4.1 Les lichens épiphytes en forêt boréale

En forêt boréale, l'abondance des lichens épiphytes, particulièrement les lichens fruticuleux[2], sur les branches des conifères des forêts relativement âgées, est souvent spectaculaire. Les lichens fruticuleux de la forêt boréale sont principalement représentés par quatre genres au Québec : *Bryoria* spp., *Usnea* spp., *Alectoria sarmentosa* et *Evernia mesomorpha*. Les espèces du genre *Bryoria*, représenté par une dizaine d'espèces au Québec, ont généralement une grande amplitude écologique par rapport aux conditions de lumière et d'humidité (Edwards et Rictcey, 1960). Elles sont tolérantes aux conditions de sécheresse, mais supportent mal les périodes d'hydratation prolongées (Campbell et Coxson, 2001; Goward, 1998). Parmi ces espèces, *B. nadvornikiana* est probablement la plus tolérante à l'ombre (Brodo et Hawksworth, 1977). *E.mesomorpha* est une espèce particulièrement abondante dans les sites ensoleillés (Boudreault *et al.*, 2002; Brodo *et al.*, 2001). *A. sarmentosa* a une distribution côtière, mais elle peut également se retrouver dans certains îlots plus humides à l'intérieur du continent (Brodo *et al.*, 2001); elle n'est toutefois pas rencontrée dans les pessières à mousses de l'Abitibi. Elle est généralement observée dans la partie inférieure de la canopée et serait tolérante à la lumière diffuse (Arseneau *et al.*, 1997; Campbell et Coxson, 2001). Hormis *Usnea longissima*, l'écologie des espèces du genre *Usnea* est peu étudiée (Esseen *et al.*, 1981; Gauslaa 1997). Selon Halonen *et al.* (1998), la plupart des espèces d'*Usnea* sont hygrophiles et photophiles, et elles se retrouvent principalement dans des endroits humides et bien éclairés. Elles sont peu abondantes dans les pessières à mousses relativement sèches de l'Abitibi.

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[2] Lichens fruticuleux : thalle en forme de tige, pendant ou buissonneux dont normalement il est difficile de distinguer la face inférieure de la face supérieure; lichens foliacés : thalle plus ou moins feuillu, nettement dorsi-ventral, qui adhère au substrat en un seul point ou en plusieurs points, parfois même presque totalement; lichens crustacés : thalle qui adhère complètement au substrat et dont le cortex inférieur fait défaut et ne peut être détaché intact sans que l'on prélève également un morceau du substrat.

0.4.2 Stades de développement des lichens épiphytes

La dispersion, la fixation au substrat et la germination des propagules, le développement juvénile des thalles, la croissance des thalles matures et la reproduction sont les étapes essentielles pour assurer la colonisation des espèces (Armstrong, 1988). Les lichens se reproduisent sexuellement grâce à la production de spores par la partie fongique ou asexuellement par la production de propagules symbiotiques, contenant à la fois le mycobionte et le phycobionte : sorédies, isidies, fragments de thalle, etc. De façon générale, les distances de dispersion qui ont été documentées pour certaines espèces sont assez faibles (5-100 m; Armstrong, 1988; Dettki, 1998; Esseen *et al.*, 1981). Les spores se disperseraient sur de plus longues distances que les sorédies et les isidies et les fragments de thalle seraient les propagules qui se disperseraient sur les plus courtes distances (Barkman, 1958; Hedenås *et al.*, 2003). Pour assurer leur dominance à l'échelle locale ainsi que la colonisation de nouveaux habitats, plusieurs espèces ont deux modes de dispersion (Gauslaa, 1997). Chez plusieurs espèces de lichens fruticuleux qui dominent la canopée des forêts de conifères (*Bryoria* spp. *Usnea* spp., *A. sarmentosa*), la fragmentation des thalles a un rôle important à jouer pour assurer la dispersion des espèces (Stevenson, 1985, 1988). Une fois arrivées sur un site, les espèces doivent retrouver les conditions favorables à l'établissement des propagules et au développement des thalles juvéniles. Les facteurs abiotiques tels que la qualité des substrats (texture et chimie de l'écorce), la disponibilité des substrats et les conditions microclimatiques influencent également l'attachement, la survie des diaspores et la croissance des espèces (Armstrong, 1988).

Les lichens sont des organismes poïkilohydriques, c'est-à-dire qu'ils n'ont pas de mécanisme pour réguler leur perte et leur gain en eau (Nash, 1996). Leur activité métabolique est directement reliée au microclimat. Leur contenu en eau, la lumière et la température sont les trois variables environnementales les plus influentes pour les lichens épiphytes. La photosynthèse des lichens peut s'effectuer que lorsqu'ils sont en même temps mouillés et

éclairés. Dans les forêts fermées, les lichens photosynthétisent rarement à leur taux maximal en raison de la faible intensité lumineuse qui prévaut dans ces forêts (Green *et al.*, 1995) et, par conséquent, l'ouverture de la canopée peut avoir une influence positive sur la croissance des lichens (Gauslaa *et al.*, 2006; Jansson *et al.*, 2009). Une hausse de la température peut aussi accroître le taux de photosynthèse des lichens, mais au-delà d'un certain seuil, le taux de respiration augmentera aussi et aura pour conséquence de diminuer la croissance des lichens (Nash, 1996). De plus en plus d'études montrent que le taux de croissance des lichens épiphytes n'est pas aussi limitant que l'on croyait pour expliquer leur faible taux d'accumulation dans les forêts (Muir *et al.*, 1997; Renhorn et Esseen, 1995). Par exemple, Gauslaa *et al.* (2007) ont observé dans les forêts boréales scandinaves des taux de croissance saisonnière allant jusqu'à 38%. Il est à noter cependant que la fragmentation des thalles a un impact négatif sur l'accumulation de biomasse, particulièrement pour les lichens fruticuleux (*Bryoria*, *Usnea* et *A. sarmentosa*; Esseen et Renhorn, 1998).

0.4.3 Association des lichens épiphytes avec les vieilles forêts

La richesse et l'abondance des lichens épiphytes sont généralement supérieures dans les vieilles forêts. Plusieurs raisons ont été évoquées pour expliquer cette lente accumulation. D'abord, l'âge du peuplement est intimement lié au développement d'une structure propice à l'établissement et à la croissance des lichens (Neitlich, 1993). Ainsi, dans les vieux peuplements, la diversité d'essences, de classes de diamètres, de hauteurs, la présence de vieux arbres, de chicots et de petites ouvertures causées par la mortalité de certains individus qui favorisent la pénétration de lumière, de propagules et d'humidité (Neitlich, 1993) sont autant de caractéristiques qui diversifient les habitats pour les lichens et qui contribuent à leur accumulation (Esseen *et al.*, 1996; Hyvarinen *et al.*, 1992; Lesica *et al.*, 1991; McCune, 1993; Tibell, 1992).

Ensuite, la longévité des substrats a une influence positive sur l'accumulation de la richesse et de la biomasse en lichens épiphytes dans les vieilles forêts puisque les substrats pourront accumuler des propagules pendant une plus longue période de temps (Boudreault *et al.*,

2002; Esseen *et al.*, 1996; Lyons *et al.*, 2000). La richesse et l'abondance en lichens épiphytes augmentent généralement avec la taille des arbres (ou la taille de la branche), non seulement parce que les gros arbres sont souvent plus vieux, mais aussi parce que leur écorce possède des propriétés physiques ou chimiques particulières plus favorables à l'établissement des lichens (Johansson et Ehrlén, 2003) ou parce que les chances d'intercepter les propagules et l'humidité augmentent avec la taille du substrat (Lyons *et al.*, 2000).

Finalement, puisque des études expérimentales ont montré que les conditions environnementales et les substrats des jeunes forêts étaient favorables à l'établissement et au développement de certaines espèces associées aux vieilles forêts (*Lobaria oregana* en Oregon [Sillett *et al.*, 2000], *L. scrobiculata* en Norvège [Hilmo et Såstad, 2001] et *Usnea longissima* en Oregon [Keon et Muir, 2002]), leur absence dans les jeunes forêts a été attribuée à leur faible potentiel de dispersion. D'ailleurs, d'autres études ont montré que l'abondance des lichens diminuait soit en fonction de la distance à la bordure d'une forêt mature résiduelle (Dettki, 1998; Dettki *et al.*, 2000; Stevenson, 1988) ou en fonction de la distance les séparant des arbres résiduels (Sillett et Goslin, 1999).

0.4.4 Impacts de l'aménagement forestier sur les lichens épiphytes

Des différences prononcées entre la biomasse et la diversité des lichens épiphytes des forêts naturelles et aménagées ont été notées (Dettki et Esseen, 1998; Esseen *et al.*, 1996). Par exemple, Esseen *et al.* (1996) ont montré que les peuplements aménagés en Suède avaient 6 fois moins de lichens épiphytes que les vieux peuplements naturels. Le modèle proposé par Dettki et Esseen (2003) prédit que seule une faible proportion de la biomasse épiphyte sera maintenue dans un paysage aménagé avec une révolution forestière de 110 ans. Plusieurs espèces ont décliné en Europe suite à l'intensification des coupes forestières. Par exemple, *Lobaria pulmonaria* (Rose, 1988) et *Usnea longissima* (Esseen *et al.*, 1981) étaient toutes deux plus fréquentes par le passé et *Erioderma pedicallatum*, presque disparue d'Europe, est maintenant confinée à quelques sites riches en sapin baumier de la Nouvelle-Écosse et de Terre-Neuve.

Quelques études ont montré que l'isolement des habitats peut avoir un impact négatif sur la colonisation de nouveaux habitats (Gu *et al.*, 2001; Johansson et Ehrlén, 2003; Öckinger *et al.*, 2004). Par exemple, Öckinger *et al.* (2004) n'ont pas observé de nouveaux sites colonisés par *L. pulmonaria* en Suède, 10 ans après leur premier suivi. Selon ces auteurs, la distance séparant les sites était trop grande pour permettre la colonisation de nouveaux sites.

Puisque l'activité métabolique des lichens est directement reliée au microclimat (Nash, 1996), les lichens peuvent être sensibles aux effets de lisière. Des études ont montré que la biomasse des lichens fruticuleux (*A. sarmentosa*, *E. mesomorpha*, *Usnea* et *Bryoria*) était significativement plus faible en bordure des coupes (jusqu'à 50 m de la bordure) qu'à l'intérieur des forêts dans les pessières de la Scandinavie (Esseen et Renhorn, 1998) et de l'Abitibi (Rheault *et al.*, 2003). Par contre, des augmentations de croissance chez certaines espèces ont été observées en bordure de coupe (p. ex., *U. longissima*; Jansson *et al.*, 2009). Le déclin de biomasse typiquement observé après la création de lisières s'expliquerait par une hausse de la fragmentation des thalles, soit par le vent ou par la neige, plutôt que par une diminution de la croissance des espèces. À l'échelle du peuplement, la biomasse en bordure des coupes peut également décliner en raison d'une diminution de substrats disponibles pour les lichens puisqu'il y a souvent moins d'arbres et moins de branches par arbre en bordure des coupes (Rheault *et al.*, 2003). Enfin, selon Kruy et Jonsson (1997), seuls les fragments de grande taille peuvent contenir assez d'habitats d'intérieur pour maintenir les espèces ayant des besoins spécifiques sur le plan de l'ombre et de l'humidité comme les espèces du groupe des Caliciales.

Plusieurs études ont montré que les coupes partielles peuvent maintenir une biomasse importante de lichens épiphytes (Coxson *et al.*, 2003; Coxson et Stevenson, 2005; Muir *et al.*, 2006; Rominger *et al.*, 1994; Stevenson et Coxson, 2003, 2006; Stone *et al.*, 2008), du moins à court terme. Puisque la croissance des lichens épiphytes est souvent limitée dans les forêts relativement fermées, les coupes partielles, en ouvrant la canopée, pourraient stimuler la croissance des lichens épiphytes (Stevenson et Coxson, 2003; Rominger *et al.*, 1994; Stone *et al.*, 2008). Par contre, des changements dans la composition des lichens ont souvent été

observés suite à l'ouverture du peuplement forestier, favorisant les espèces plus généralistes au détriment des espèces plus tolérantes à l'ombre (Rominger *et al.*, 1994; Stone *et al.*, 2008). Enfin, d'autres études ont trouvé des effets négatifs associés aux coupes partielles sur la croissance et la vitalité de certaines espèces (Coxson et Stevenson, 2005; Hedenås et Ericson, 2003; Lõhmus *et al.*, 2006).

0.5 Objectifs et structure de la thèse

Dans un contexte d'AFE, il est essentiel d'acquérir des connaissances sur les lichens épiphytes qui sont vulnérables à la perte d'habitat, aux modifications des conditions locales du milieu et à la fragmentation des habitats. L'objectif principal de cette thèse est de mieux comprendre les processus de développement des populations de lichens épiphytes dans les pessières à mousses de l'Abitibi, d'évaluer les impacts de diverses pratiques sylvicoles (coupes totales et partielles) sur ces populations et d'identifier les caractéristiques structurales à diverses échelles spatiales qu'il faut conserver ou recréer par l'aménagement forestier afin de préserver leur biodiversité et leur rôle fonctionnel dans cet écosystème (p. ex., cycle des éléments nutritifs, nourriture et abris pour les animaux).

Cette thèse est composée de quatre articles. Le premier chapitre a été réalisé à l'intérieur de forêts naturelles dans le but de décrire les patrons d'accumulation de lichens épiphytes et de cerner quels pourraient être les effets de la raréfaction des vieux peuplements sur les lichens épiphytes. Les chapitres 2 et 3 réfèrent à divers aspects de l'aménagement par coupe totale et de la configuration des habitats résiduels laissés dans les agglomérations de coupes totales. Le chapitre 2 porte sur la capacité de divers habitats résiduels à maintenir les populations de lichens épiphytes et sur les effets de lisière à l'intérieur des forêts résiduelles. Dans le chapitre 3, nous abordons la question de la recolonisation des aires de coupe totale à partir des forêts résiduelles. Le quatrième chapitre vise à évaluer l'utilisation des coupes partielles comme outil d'AFE de la pessière en étudiant la réponse de deux espèces de lichens à l'ouverture du couvert forestier.

Plus spécifiquement, l'objectif du premier chapitre est de décrire l'influence du temps écoulé depuis le dernier feu, de la structure du peuplement, de la taille et de l'âge des arbres et de la hauteur des branches sur la biomasse de lichens épiphytes fruticuleux. Cette étude a été menée dans la pessière à mousses de la portion Ouest de l'Abitibi dans divers sites âgés de 50 à plus de 200 ans. J'ai utilisé des données de biomasse de trois genres de lichens (*Bryoria*, *Evernia* et *Usnea*). La particularité de cette étude est d'avoir quantifié la biomasse à l'échelle de l'arbre, ce qui permet d'avoir des estimés de biomasse à l'échelle des peuplements. Cette étude permet notamment d'évaluer l'importance relative des différents stades forestiers pour le maintien des lichens épiphytes fruticuleux dans une perspective d'AFE.

Le deuxième chapitre vise à évaluer la qualité de divers types de forêts résiduelles pour le maintien de la biomasse en lichens épiphytes fruticuleux et à comparer les effets de lisière entre différents types de forêts résiduelles. Quatre types d'habitat résiduel ont été étudiés, soit des séparateurs de coupe, des bandes riveraines, des grands blocs de forêts résiduelles et des forêts intérieures servant de contrôle. J'ai ensuite évalué si les effets de lisière étaient plus importants dans des habitats résiduels linéaires étroits avec deux bordures (séparateurs de coupe) comparativement à des habitats plus grands possédant une seule bordure (grands blocs de forêts résiduelles). Cette étude a été réalisée dans des peuplements matures et surannés de la pessière à mousses de la portion Est de l'Abitibi. J'ai utilisé des données de biomasse des lichens des genres *Bryoria*, *Evernia* et *Usnea*. Cette étude permet d'évaluer si la taille des forêts résiduelles est adéquate pour préserver les populations de lichens épiphytes.

Dans le troisième chapitre, je compare la colonisation de diverses espèces de lichens dans deux types de peuplements en régénération issus de coupes totales, soit des peuplements régénérés naturellement et des plantations. Je veux également évaluer si le taux de colonisation diminue à mesure que l'on s'éloigne d'un peuplement adjacent non coupé, s'il augmente avec le temps écoulé depuis la coupe et s'il augmente à proximité de vieilles forêts. Cette étude a été réalisée dans la pessière à mousses de l'Est de l'Abitibi. Cette fois-ci, les analyses portaient sur des données de nombre de thalles et de recouvrement par espèce, à la fois de lichens foliacés et de lichens fruticuleux. En plus de fournir des indications quant au

potentiel de dispersion et de colonisation des espèces, cette étude nous fournit des indications quant à la capacité des deux types de peuplement en régénération rencontrés dans les aires aménagées par coupe totale à maintenir les populations de lichens épiphytes.

Dans le dernier chapitre, j'ai étudié les effets des coupes partielles sur la croissance de deux espèces de lichens épiphytes. Le but de cette étude était d'évaluer si l'ouverture de la canopée par les coupes partielles crée des conditions de croissance adéquates pour deux espèces de lichens épiphytes aux exigences écologiques différentes (*B. nadvornikiana* et *E. mesomorpha*). L'étude a été entreprise dans le réseau de coupes partielles mis en place dans les portions Ouest et Est de l'Abitibi (Fenton *et al.*, 2008). L'étude a été menée sur une période de deux ans dans un grand nombre de placettes et à l'aide d'un grand nombre de transplants. Des données microclimatiques et des photo-hémisphériques ont été analysées afin d'expliquer les patrons de croissance observés. Des analyses de viabilité ont aussi été réalisées à la fin de l'analyse dans le but de déceler si les lichens avaient subi des stress physiologiques. Cette étude vise à évaluer l'efficacité écologique des coupes partielles comme outil d'aménagement forestier écosystémique.

CHAPITRE I

FACTORS CONTROLLING EPIPHYTIC LICHEN BIOMASS DURING POSTFIRE SUCCESSION IN BLACK SPRUCE BOREAL FORESTS

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1.1 Résumé

Les lichens alectorioides forment le groupe dominant de lichens épiphytes dans les forêts boréales. Leur richesse et leur abondance augmentent généralement en fonction de l'âge et de l'hétérogénéité d'un peuplement. L'objectif de cette étude consistait à évaluer l'impact du temps depuis le dernier feu, de la structure du peuplement, de la taille et de l'âge des arbres ainsi que la hauteur des branches sur la biomasse de lichens épiphytes dans la forêt boréale de l'Ouest du Québec. Nous avons échantillonné 12 sites appartenant à quatre stades de développement (de 50 à >200 ans). Nous avons estimé la biomasse de trois groupes de lichens épiphytes (*Bryoria*, *Evernia* et *Usnea*) sur 12 arbres dans chaque site. Nos résultats ont montré que la biomasse de *Bryoria* et d'*Usnea* était plus élevée dans les stades intermédiaires de développement (entre 101 et 200 ans) comparativement aux plus jeunes (50–100 ans) et plus vieux stades (>200 ans). La biomasse des trois groupes était supérieure sur les arbres de plus gros diamètres (>16 cm) comparativement aux plus petits arbres (<16 cm). Ces résultats indiquent que la protection des peuplements après feu âgés de 101 à 200 ans devrait être priorisée afin de maintenir le rôle fonctionnel des lichens épiphytes dans les paysages aménagés.

1.2 Abstract

Alectorioid lichens are the dominant group of epiphytic lichens in boreal forests. Epiphytic lichen richness and abundance generally increase with stand age and within-stand heterogeneity. The objective of this study was to evaluate the importance of time elapsed since the last fire, stand structure, tree size, tree age, and branch height for epiphytic lichen biomass of the boreal forest of western Quebec. We sampled 12 sites belonging to four forest age classes (from 50 to >200 years). We assessed epiphytic lichen biomass of three species groups (*Bryoria*, *Evernia*, and *Usnea*) on 12 trees in each site. Our results showed that biomass of *Bryoria* and *Usnea* was higher in intermediate stages (between 101 and 200 years) compared with younger (50–100 years) and older (>200 years) stages. Biomass of the three species groups was greater on larger diameter trees (>16 cm) compared with smaller ones (<16 cm). These results indicate that the protection of postfire stands aged between 101 and 200 year should be prioritized to maintain the functional role of epiphytic lichens in managed landscapes.

1.3 Introduction

Fires play a predominant role in initiating stand succession in boreal forests (Payette, 1992). In western Quebec, postfire succession is generally characterized by the progressive replacement of young, relatively dense even-aged black spruce (*Picea mariana* (Mill.) BSP) stands by more open stands with irregular structure that are mostly dominated by the same species. In this area, the flat topography, the presence of clay soils, and the cold climate also favour an accumulation of the organic matter with time (the process of paludification; Fenton *et al.*, 2005; Simard *et al.*, 2007). As a result of this process, old forests (>200 years) are often paludified and relatively unproductive compared with younger stands because the organic layer is a poor substrate for tree growth compared with mineral soil (Simard *et al.*, 2007). Because these different postfire successional stages are likely to represent different habitat qualities for the various organisms present in boreal forests, understanding the relationships between successional types and biodiversity is a priority before sustainable management practices can be implemented.

Epiphytic lichens are an ubiquitous group in boreal forests. Within epiphytic lichens, alectorioid lichens of the genus *Alectoria*, *Bryoria*, *Usnea*, and *Evernia* are dominant on conifer branches (Brodo and Hawksworth, 1977; Esseen *et al.*, 1997). However, in the eastern boreal forest of Canada, the ecology of these groups is still relatively poorly understood (e.g., Arseneau *et al.*, 1997; Boudreault *et al.* 2002; Laflamme-Lévesque *et al.*, 1983), and knowledge of consequences of even-aged management on these organisms are even more limited (Boudreault *et al.*, 2008; Rheault *et al.*, 2003). Nonetheless, epiphytic lichens are known to play an important role within the ecosystems. During winter for example, when the snow pack is deep and the terricolous lichens inaccessible, woodland caribou (*Rangifer tarandus* (L., 1758)) feed on epiphytic lichens, mainly *Bryoria* spp. (Edwards and Ritcey, 1960; Rominger *et al.*, 1996). *Bryoria* are also an important part of vole and northern flying squirrel (*Glaucomys sabrinus* (Shaw, 1801)) diets (Sharnoff and Rosentreter, 1998). Many invertebrates feed on lichens or use lichens as shelter (Gunnarsson

et al., 2004). Lichens are part of many food webs that include invertebrates and their predators. For example, decline of songbirds in Sweden was associated with a reduction of invertebrates through a reduction in lichen abundance due to forestry (Pettersson *et al.*, 1995). Lichens are also used by animals for nest building: *Bryoria* are used by northern flying squirrel and *Usnea* by the northern parula (*Parula americana* (L., 1758)) (Sharnoff and Rosentreter, 1998). Other ecological processes may be altered by epiphytic lichen decline. For instance, epiphytic lichens contribute to nutrient cycle by absorbing the nutrients in the air and releasing them into the ecosystem as leachates and litterfall (Knops *et al.*, 1991).

At the stand scale, epiphytic lichen richness and abundance generally increase with stand age and within-stand heterogeneity (Esseen *et al.*, 1996; Lesica *et al.*, 1991; McCune, 1993). Factors such as substrate availability, longevity, and diversity (Arseneau *et al.*, 1997; Esseen *et al.*, 1996; Hilmo, 1994), as well as environmental factors such as light penetration (McCune, 1993; Neitlich, 1993), are attributed to patterns of lichen abundance and richness. Differences in lichen communities between stand types could also be explained by the relative abundance of trees with different sizes, crown structures, and branch characteristics. For instance, large trees have a larger biomass of epiphytic lichens than small trees (Campbell and Coxson, 2001; Lyons *et al.*, 2000; McCune, 1993); biomass increases generally with branch age, diameter, and length (Arseneau *et al.*, 1997; Esseen *et al.*, 1996; Goward, 1998); peak of biomass is usually found at intermediate tree height (Arseneau *et al.*, 1997, Lang *et al.*, 1980; Lui *et al.*, 2000); and vertical zonation of epiphytic communities related to gradients in canopy microclimate and changes in tree structure with tree height is often observed (Arseneau *et al.*, 1997; Campbell and Coxson, 2001; McCune, 1993).

The general objective of this study is to better understand the importance of the various forest stand ages for epiphytic lichens to choose appropriate silvicultural and conservation approaches to maintain their abundance and to preserve the ecological processes associated with epiphytic lichens in managed landscapes. In the context of the Clay Belt area acquiring such knowledge is particularly urgent for stand types aged between 101 and 200 years old, which are subjected to a very high harvesting pressure because they contain a high wood

volume compared with relatively immature stands and old paludified stands (Simard *et al.*, 2007). The specific objectives of this study were to compare biomass of three lichen taxa (*Bryoria*, *Evernia*, and *Usnea*) across classes of time elapsed since the last fire at three levels: the stand, tree, and branch levels. Following what has been mentioned in the literature, our main hypothesis is that large and old trees of overmature uneven-aged forests in this forest ecosystem will have the larger biomass of epiphytic lichens. With increasing forest stand age, we expected an increase in substrate quality for epiphytic lichens (larger and older trees) but a decrease in substrate quantity (stem density) mainly due to canopy openings.

1.4 Methods

1.4.1 Study area

The study was undertaken in a black spruce – feathermoss forest in the northwestern part of the Abitibi region of Quebec (49°00′–50°00′N, 78°30′–80°00′W). This region is part of the northern Clay Belt, a broad physiographic unit characterized by lacustrine deposits from the proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). Clay soils are predominant in the region, the topography is relatively flat, and the forest mosaic is dominated by black spruce stands (Rowe, 1972). At the southern part of the study area (weather station located at La Sarre) and in the northern part of the study area (weather station located at Matagami), mean annual temperature (1971–2000) are, respectively, 0.7 and –0.7 °C, mean annual total precipitation (1971–2000) are, respectively, 890 and 906 mm, and mean annual total snow precipitation are, respectively, 247 and 314 cm (Environment Canada, 2000).

1.4.2 Lichen species in the study

We studied fruticose epiphytic lichens because they are the dominant epiphytic group in natural boreal forests. The three genera of fruticose lichens that we studied are *Bryoria*, *Usnea*, and *Evernia*, the only taxa of fruticose lichens present in the study sites. The most common and abundant *Bryoria* and *Usnea* species in our study area were *Bryoria trichodes* (Michx.) Brodo & D. Hawksw. subsp. *trichodes* and *Usnea filipendula* Stirt., *Bryoria*

nadvornikiana (Gyeln.) Brodo & D. Hawksw., *Bryoria furcellata* (Fr.) Brodo & D. Hawksw., *Bryoria lanestris* (Ach.) Brodo & D. Hawksw., *Usnea hirta* (L.) F.H. Wigg., and *Usnea subfloridana* Stirt. were also frequently observed (unpublished data). Although present in the study area, *Usnea longissima* Ach. was encountered infrequently. *Evernia mesomorpha* Nyl. is the only species of the genus that was present in our study area. Other common epiphytic lichens in the forest stands that we sampled were *Hypogymnia physodes* (L.) Nyl., *Tuckermannopsis americana* (Spreng.) Hale, *Parmeliopsis ambigua* (Wulfen) Nyl., *Parmeliopsis hyperopta* (Ach.) Arnold, *Mycoblastus sanguinarius* (L.) Norman, and *Japewia tornoensis* (Nyl.) Tønsberg.

1.4.3 Sampling

Based on a previous fire history reconstruction by Lecomte *et al.* (2005), 12 stands distributed across four age-classes (50–100, 101–150, 151–200, and >200 years) were selected for this study (see Appendix 1.1). This study is based on the assumption that stands of different ages represent a post-fire successional sequence. The chronosequence has been validated via stem analysis (Lecomte *et al.* 2006). *In situ* analysis of the forest floor and detailed analyses of slope, soil texture, and fire severity were undertaken to insure that initial conditions were similar for all stands (for more details on site selection see Lecomte *et al.* 2005).

For all stands, diameters at breast height (DBHs) of all trees within a circular plot of 400 m^2 were measured to calculate stem density and basal area. These plots of 400 m^2 are refered to the 'stand level' for the rest of the chapter. To study the within-stand and within-tree epiphytic lichen distribution, we randomly selected three trees for each DBH class (8.0–12.0, 12.1–16.0, 16.1–20.0, and >20 cm), for a total of 12 trees per stand and 144 trees for the study. However, because it was not always possible to find three trees per class within the plot, the number of trees per DBH class varied in the analyses.

The trees were felled and the number of branches (>50 cm long) in three canopy height classes (lower canopy, 0–5.0 m from ground level; intermediate canopy, 5.1–10.0 m; and

upper canopy, 10.1–15.0 m) were counted. Within each height class, we systematically collected the branches longer than 50 cm that were closest to 1.5, 3.0, and 4.5 m above the lower limit of each class (i.e., three branches per height class per tree). We then measured the length of each branch, assessed its vitality (dead or live), and evaluated the proportion of the branch covered with bark in three classes (on <30%, 30%–70%, and >70% of the branch surface). In some cases, few branches were present in the lower height class or in the higher height class and only one or two branches per class were collected. A total of 831 branches were brought back to the laboratory. At the base of all trees, one disk was collected, and growth rings were counted to assess the age of the trees.

In the laboratory, the lichens were sorted by taxa (*Bryoria* spp., *E. mesomorpha*, and *Usnea* spp.) and weighed (to the nearest 0.0001 g) after drying at 60 °C for 24 h. This was done on all branches for *E. mesomorpha* and *Usnea* spp. Because *Bryoria* spp. were much more abundant, this taxon was sorted on a subset of 473 branches selected randomly within each height class and each tree. On the remaining 347 branches, the *Bryoria* spp. biomass was estimated by the clump method, which consists in visually comparing lichen accumulations on a given branch to standard units of lichen of known mass (Campbell *et al.*, 1999); thus, lichen mass is estimated according to how many standard units are present on that branch. We conducted linear regression between the estimates and lichen biomass measures on a subset of 88 branches, and we used the regression equation to correct the *Bryoria* estimates. The estimates and the measured biomass values were natural log transformed ($\ln X + 1$) prior to the analyses to conform to the normality and homoscedasticity assumptions of regressions. Bias introduced by correcting estimates with natural log transformed data was corrected by adding a constant ($s^2/\sqrt{n}$) to the regression equation (see Campbell and Coxson, 2001). The resulting equation ($\ln (Y + 1) = Y_0 + a \times \ln (X + 1) + (s^2/\sqrt{n})$) was applied to the estimates of lichen biomass, where Y is the regression corrected lichen biomass for each branch, X is the estimated lichen biomass for each branch, and is the natural lognormally distributed errors. The regression equation was $\ln (Y + 1) = 0.1667 + 1.7419 \times \ln (X + 1) + 0.0043$; $r^2 = 0.884$. The antilog of the outputs of the regression was calculated to convert the estimates to grams per branch.

1.4.4 Statistical analyses

Biomass values across age and DBH classes were analysed (*i*) at the branch level, (*ii*) at the tree level, and (*iii*) at the stand level. Lichen biomass at the branch level for each taxa was analysed using a nested two-way analysis of variance (ANOVA) model. Age and DBH classes were fixed factors; sampling site was a random factor nested within age class; and sampling tree was a random factor nested within the interaction of sampling site, DBH class, and age class. Response variables were the biomass per branch for each lichen taxa. Three outlier values for mass of *Bryoria* were removed (11.7, 18.5, and 25.0 g). Analyses were performed with the MIXED procedure of SAS (SAS Institute Inc. 2002). Denominator degrees of freedom were calculated using Satterthwaite's approximation (Littell *et al.*, 1996). Because the MIXED procedure does not compute an F test for the variance component of random effects, the significance of the random effect was calculated with the likelihood ratio statistic, which was computed by taking the difference between the –2 restricted maximum likelihood estimator log-likelihood of the model containing the random effect and the model without the random effect, as suggested by Littell *et al.* (1996). Significant differences ($p \leq 0.05$) between classes in all ANOVAs analyses were detected with least squares means Tukey honest significant difference tests. Data were square-root transformed ($x^{0.5} + (x + 1)^{0.5}$) to satisfy the normality and homoscedasticity of the ANOVAs. Differences in branch length between age and DBH classes were also tested with the same nested two-way ANOVA model.

Mean biomass values, mean branch length, and number of branches per height class were compared among height classes with one-way ANOVAs. Biomass values were rank transformed, and branch lengths were log transformed to satisfy the assumptions of ANOVAs. We also ran one-way ANOVAs with branch length as a covariate to evaluate if the effect of height class was still significant after controlling for branch length.

To estimate the biomass per tree (n = 144), the biomass of each lichen taxa in each height class was calculated by multiplying the number of branches by the mean biomass per branch in that height class, and the biomasses from all height classes were subsequently added up.

Nested two-way ANOVA models were used to compare lichen biomass at the tree level among age classes and DBH classes. Age class and DBH class were fixed factors, and sampling site was nested within age class (random factor). Satterthwaite's approximation was used to calculate the denominator degrees of freedom (Littell *et al.*, 1996). Logarithmic transformations of *Bryoria*, *Evernia*, and *Usnea* data were applied to meet the assumptions of ANOVA. We also used nested two-way ANOVA models to compare tree age, tree height, and number of branches per tree between age and DBH classes (fixed factors) with sampling site nested within age class (random factor).

To explore the relationships between *Bryoria*, *Evernia*, and *Usnea* biomass and tree age by controlling the influence of tree DBH, we performed linear or polynomial regressions between the residuals of the regressions between biomass values and tree DBH against tree age. Relationships between tree DBH and biomass values without the influence of tree age were also explored by regressing the residuals from the regressions between biomass values and tree age against tree DBH. Because tree height was highly correlated with tree DBH (see Table 1.1), results of the partial regressions between tree height and biomass values are not presented.

The biomass estimated at the tree level of each species group was converted to biomass at the stand level (400 m^2) by attributing the mean biomass of that DBH class and age class combination to each tree from a given DBH class present in the stand. Total stand biomass was the summation of all tree biomass values. Stand biomass was then converted to biomass per hectare. One-way ANOVAs were used to test for differences in biomass at the stand level (per hectare) among age classes. Differences in overall stem density and basal area of sampled stands were also tested among age classes with one-way ANOVAs.

1.5 Results

1.5.1 Stand, tree, and branch characteristics

Significant differences in stem density and basal area among age classes were detected by ANOVAs (tree density: $F_{3,11} = 5.16$, $p = 0.028$; basal area: $F_{3,11} = 9.42$, $p = 0.005$). Tree density and basal area were highest in stands between 50 and 100 years old, but differences were only significant in stands >200 years old for stem density and in stands >150 years old for basal area (Table 1.1). Stem density and basal area were strongly positively correlated ($r = 0.911$, $p < 0.001$, $n = 12$). Spearman correlations between variables measured at the tree level are shown in Table 1.2. Tree height was positively correlated with tree DBH and number of branches per tree. Branch number showed a negative correlation with tree age and a positive correlation with tree DBH. Tree age was higher in older stands, and the smaller trees were significantly younger (Tables 1.1 and 1.3). Tree height did not vary according to age classes but increased with tree DBH (Tables 1.1 and 1.3). Branch length varied with tree DBH but not within age classes (Table 1.4). Branches were longer on trees >16 cm DBH (Table 1.1). Branches were significantly shorter in the upper canopy ($F_{2,394} = 10.57$, $p < 0.001$) (Table 1.1). Age class and tree DBH had a significant effect on the number of branches (Table 1.3), with youngest stands and trees >16 cm DBH having the highest number of branches (Table 1.1). Number of branches also varied among height classes ($F_{2,395} = 55.16$, $p < 0.001$) with highest values in height class 5.1–10.0 m, followed by height-class 10.1–15.0 m and height-class 0–5.0 m (Table 1.1).

1.5.2 Lichen biomass at the branch level

Pooled over the 12 sites, *Bryoria* biomass per branch (0.715 ± 1.455 g; mean ± SD) was 10.4 and 44.7 times higher than *Evernia* (0.069 ± 0.133 g) and *Usnea* (0.016 ± 0.044 g), respectively. *Bryoria* occurred on 87.8% of the sampled branches compared with 72.6% for *Evernia* and 52.0% for *Usnea*. There was twice more *Bryoria* and 1.3 times more *Evernia* on live branches compared with dead branches; however, there was no difference for *Usnea*. Branches covered by bark (on >70% of the branch surface) had 2.7, 2.3, and 1.6 times more *Bryoria*, *Usnea*, and *Evernia*, respectively, compared with branches with 30%–70% of bark

and 4.1, 5.0, and 1.7 times more *Bryoria*, *Usnea*, and *Evernia*, respectively, than branches with almost no bark (on <30% of the branch surface). Percentages of branches with bark (>70%) is greater in the 5.1–10.0 m (88.5%) and 10.1–15.0 m (98.8%) height classes compared with the 0–5.0 m height class (44.9%).

Nested two-way ANOVAs revealed that biomass per branch differed significantly among age classes for *Bryoria* and *Usnea* and among DBH classes for all lichen taxa (Table 1.4). *Bryoria* biomass was significantly lower in 50–100 year class (Fig. 1.1a). *Usnea* biomass was higher in stands between 101 and 200 years old compared with stands between 50 and 100 years and >200 years old (Fig. 1.1a). The lowest biomass of *Bryoria* per branch was found on trees between 8 and 12 cm DBH (Fig. 1.1b). Biomass of *Evernia* and *Usnea* were higher on trees >16 cm DBH (Fig. 1.1b).

Biomass of the three taxa varied among the height classes (*Bryoria*: $F_{2,394} = 10.08, p < 0.001$; *Evernia*: $F_{2,394} = 3.40, p = 0.034$; *Usnea*: $F_{2,394} = 8.20, p < 0.001$); they all had more biomass in height class 5.1–10.0 m (Fig. 1.2). When branch length was added as a covariate in the models, the height classes were still significantly different for *Bryoria* and *Usnea* (*Bryoria*: $F_{2,393} = 8.43, p < 0.001$; *Evernia*: $F_{2,393} = 0.95, p = 0.39$; *Usnea*: $F_{2,393} = 4.79, p = 0.009$), but the differences were significant only between the 0–5.0 m and 5.1–10.0 m classes. Branch length had a significant positive influence on lichen biomass (*Bryoria*: $F_{1,393} = 52.89, p < 0.001$; *Evernia*: $F_{1,393} = 51.50, p < 0.001$; *Usnea*: $F_{1,393} = 77.57, p < 0.001$).

In the youngest age class, the percentages of the total lichen biomass occupied by *Bryoria* and *Evernia* were lower (75.2%) and higher (22.9%), respectively, compared with the other age classes (overall means: *Bryoria* = 91.2%; *Evernia* = 6.9%).

1.5.3 Lichen biomass at the tree level

At the tree level, age class had a significant effect on the biomass of *Bryoria*, and tree DBH had a significant effect on the biomass of all lichen taxa (Table 1.5). Biomass of *Bryoria* was significantly higher on trees from age classes 101–150 and 151–200 years compared with

trees from age classes 50–100 and >200 years (Fig, 1.3a). *Bryoria* biomass in age class 50–100 years was particularly low with biomasses that are at least 3.7 and 4.9 times lower compared with biomasses observed in age classes 101–150 and 151–200 years, respectively (Fig. 1.3a). Biomasses of *Bryoria*, *Usnea*, and *Evernia* were significantly higher on trees from DBH classes 16.1–20.0 and >20 cm (Fig. 1.3b).

Regressions analyses between the residuals (from the regressions between biomass values and tree age) and tree DBH are significant for the three taxa (*Bryoria*: $r^2 = 0.287$, $p < 0.001$; *Evernia*: $r^2 = 0.253$, $p < 0.001$; *Usnea*: $r^2 = 0.212$, $p < 0.001$, Fig. 1.4). Biomass of the three taxa increased linearly with tree DBH (Fig. 1.4). Relationships between the residuals (from the regression analyses performed between tree DBH and biomass values) and tree age showed a significant quadratic relationship with tree age for *Bryoria* and *Usnea* (*Bryoria*: $r^2 = 0.285$, $p < 0.001$; *Evernia*: $r^2 = 0.007$, $p = 0.629$; *Usnea*: $r^2 = 0.086$, $p = 0.002$; Fig. 1.4). The biomass of these taxa first increased with tree age from 50 to approximately 150 years and then decreased on trees >150 years old (Fig. 1.4).

1.5.4 Lichen biomass at the stand level

Biomasses of *Bryoria*, *Evernia*, and *Usnea* at the stand level were 133.1 ± 72.7 kg/ha, 11.5 ± 5.0 kg/ha, and 2.8 ± 1.9 kg/ha, respectively. Biomasses of *Bryoria*, *Evernia*, and *Usnea* at the stand level varied significantly with age classes (Table 1.6). *Bryoria* and *Usnea* biomass were lower in 50–100 year and >200 year classes and higher in 101–150 year and 151–200 year classes, whereas *Evernia* biomass was lower in >200 year class (Table 1.6).

1.6 Discussion

Results from this study showed that lichen biomass is overwhelmingly dominated by *Bryoria* in black spruce forests of the Clay Belt; this genus is generally more abundant by a factor of ≥10 compared with *Evernia* and *Usnea*. Nonetheless, the three lichen taxa appear to share relatively similar ecological niches; for example, biomass at the stand level of both *Bryoria* and *Usnea* was higher in mature and overmature (~101–200 years) stands compared with

younger (50–100 years) and older (>200 years) stands. This pattern contrasts with what is generally reported in boreal ecosystems, i.e., a maximal abundance of epiphytic lichens in later age classes (Dettki and Esseen, 1998; Esseen *et al.*, 1996; Hyvarinen *et al.*, 1992). Lichen biomass was also higher for the three lichen taxa on large trees, and in midcrown positions. In the following sections, we will examine the mechanisms responsible for these trends at the stand, tree, and branch scales.

1.6.1 Effect of stand characteristics on epiphytic lichen biomass

The gradient of time since fire is related to the gradients of light and humidity and to the development of a stand structure favourable for lichen establishment and growth (Lehmkuhl, 2004; Neitlich, 1993; Sillett and McCune, 1998). Contrary to young dense and even-aged stands, the more open and diverse structure of old forests allows a greater penetration of light and humidity (Geiger, 1965; McCune, 1993; Neitlich, 1993) and favours the colonization and accumulation of lichen biomass (Lehmkuhl, 2004; Uliczka and Angelstam, 1999). Many studies have suggested that light increase in canopy openings following natural disturbance or stand thinning increased lichen epiphytic growth and diversity (Neitlich and McCune, 1997; Peterson and McCune, 2001; Stevenson and Coxson, 2007). Additionally, low light levels in young stands may compromise lichen establishment via limitations on hyphal growth (Hilmo and Såstad, 2001) and lichen growth if respiration is favoured to the detriment of photosynthesis (Uliczka and Angelstam, 1999). However, in circumstances where canopies are very open, lichen biomass accumulation can be greatly reduced. This can be attributed to two factors. Firstly, when canopy openings are very abundant, tree density is often very low, leading to reduced availability of substrates for colonization by epiphytic lichens (Jaakkola *et al.*, 2006). Very low tree densities occur in our study in the >200 year age class compared with 50–100 and 101–150 year age classes (Table 1.1) because of paludification, which inhibits the recruitment and the growth of young trees in older forests (Lecomte *et al.*, 2006). Secondly, when canopy gaps are too large and (or) develop rapidly, this can lead to environmental conditions that become unfavourable for lichen biomass accumulation. Greater wind penetration in very open stands, in particular, can lead to fragmentation of epiphytic lichens, limiting biomass accumulation. Increases in light and

temperature may also damage chlorophyll, reduce the duration of hydration episodes in lichens, and decrease the photosynthesis rate (Gauslaa and Solhaug, 1996; Nash, 1996). This may explain why we observed a decline of *Bryoria* and *Usnea* biomass at the branch and tree levels in >200-year-old stands compared with 101- to 200-year-old stands.

According to many authors, propagule dispersal would be the most critical phase in the life cycle of many lichens, and forest continuity has been identified as a very important factor in increasing the probability of successful propagule dispersal and establishment (Dettki *et al.*, 2000; Hilmo and Såstad, 2001; Stevenson, 1988). For example, in the case of *Bryoria*, dispersal is insured by fragments that break from the main thallus by the action of wind, rain, or ice (Dettki, 1998; Esseen, 1985; Stevenson, 1988). Those relatively large fragments are less efficient than spores or small vegetative propagules for long-distance dispersal (e.g., isidia and soredia) (Dettki, 1998; Esseen *et al.*, 1996; Peterson and McCune, 2001). However, as observed for *U. longissima* (Gauslaa *et al.* 1998), *Bryoria* fragments may insure within-stand dispersal efficiently; once established within a stand, the population may increase relatively quickly. *Usnea* have a central cord that make them more resistant to fragmentation. Thus, for most *Usnea* species, dispersal is mostly insured by soredia (Halonen *et al.*, 1998). Our results show that *Usnea* species were more frequently encountered within stands between 101–150 and 151–200 years old than within stands between 50 and 100 years old, and thus, a colonization delay could also explain their lower biomass in young stands. However, poor light conditions may also be responsible of the low abundance of *Usnea* in young stands. In fact, according to Halonen *et al.* (1998), *Usnea* are photophilous species and are preferentially found in well-lit habitats. Similarly, *E. mesomorpha* was abundant in our 50- to 100-year-old stands. *Evernia mesomorpha* is a species that disperses mainly from soredia, although spores are sometimes observed (Piercey-Normore, 2006) and would have better long-distance dispersal capabilities than either *Usnea* or *Bryoria*. Although *E. mesomorpha* is often found in open forests (Brodo *et al.*, 2001), our results suggest that more shaded habitats (such as our 50- to 100-year-old stands) are also conducive to growth of this species.

1.6.2 Impacts of tree age and tree size on epiphytic biomass

Many studies have shown a relationship between tree age and epiphytic lichen biomass (Boudreault *et al.* 2000, 2002; Esseen *et al.* 1996). Old trees generally host a more abundant epiphytic flora for at least two reasons. Firstly, they are exposed to colonization for longer periods, thus increasing their chance of being successfully colonized by lichen propagules. Secondly, substrate and microclimate instability induced by tree growth decreases with time, which can also favour lichen establishment and biomass accumulation (Neitlich, 1993; Stevenson, 1985). For example, Uliczka and Angelstam (1999) have shown that conifers with a slower growth rate have a greater number of species than conifers with a faster growth rate. On the other hand, our results showed that the relationship between tree age and epiphytic biomass is not linear: beyond 150 years old, *Bryoria* and *Usnea* biomass per tree tends to decline. The decrease in branch number due to branch mortality with tree aging could explain the decrease of epiphytic biomass on older trees as hypothesized by Rolstad and Rolstad (1999). Our results support this hypothesis because the number of branches decreased as a function of tree age (see Table 1.2). Low abundance of lichens in younger stands (between 50 and 100 years) compared with older stands may also partly be explained by tree age, because trees in stands between 50 and 100 years old had avout half the age of trees located in stands between 100 and 150 years old (see Table 1.2).

Epiphytic biomass is generally higher on trees with larger DBH (Campbell and Coxson, 2001; Lyons *et al.*, 2000; McCune, 1993). Longer branches, higher numbers of branches, and higher tree heights may explain the higher biomass observed on large-diameter trees (>16 cm) compared with small-diameter trees (<16 cm) in this study. Large trees may also have a better capacity to intercept propagules, nutrients, and humidity than small trees (Lyons *et al.*, 2000), and their bark may have chemical and physical properties (e.g., rougher bark) more favourable to lichen establishment and interception of lichen propagules than small trees (Johansson and Ehrlén, 2003).

1.6.3 Impacts of branch height and branch characteristics on epiphytic biomass

Vertical zonation of epiphytes related to gradients of light and humidity has been observed in many studies (e.g., Campbell and Coxson, 2001; Coxson and Coyle, 2003; McCune, 2000). For example, many authors have found that *Bryoria* spp. biomass increases, whereas *Alectoria sarmentosa* (Ach.) Ach. biomass decreases with tree height (Arseneau *et al.*, 1997; Campbell and Coxson, 2001; Coxson and Coyle, 2003). In part, differences in the level of tolerance to duration of hydration could be responsible for this zonation (Campbell and Coxson, 2001; Coxson and Coyle, 2003; Goward 1998). Lichens located in the lower canopy are exposed to more uniform humidity conditions. Those in the upper canopy are generally exposed to a drier environment; even if they are hydrated more often, they also dried more quickly (McCune, 1993). Results of this study indicate that *Bryoria* and *Usnea* are significantly more abundant in the intermediate canopy, and no distinct vertical zonation among the species groups has been observed. Because tree heights were relatively small in our study compared with those reported elsewhere (e.g., 25 m in Campbell and Coxson, 2001 and up to 65 m in McCune, 1993), it is possible that differences in environmental conditions between the three height classes were not large enough to create distinct ecological niches.

The peak of *Bryoria* and *Usnea* biomass in the intermediate canopy may reflect the species' ecological requirements and branch quality (e.g., branch vitality, branch length, and number of branches). In the intermediate height stratum, branches were longer than in the higher stratum; these branches are also lower on the tree, and thus older, and conditions of humidity and sunlight were probably more stable than in the higher stratum. Microclimatic conditions such as higher wind exposure and snow accumulation have been evoked to explain the low accumulation of epiphytic lichens on branches of the top of the trees (Arseneau *et al.*, 1997). Our results suggest that variation in lichen biomass between intermediate and upper positions for *Bryoria*, *Usnea*, and *Evernia* is mostly influenced by branch size and the number of branches rather than by microclimatic conditions. When branch length is integrated as a covariate in the models, differences between intermediate and upper positions were no longer significant. Thus, *Bryoria* and some species of *Usnea*, which are adapted to moderately dry to dry environments (Brodo and Hawksworth, 1977; Edwards and Ritcey, 1960; McCune,

1993), may colonize and have high biomass accumulation rates in branches of the upper stratum (when individual thalli are considered) (Arseneau *et al.*, 1998), but the fact that branches are shorter in that stratum seems to limit overall lichen accumulation. In lower canopy positions, the low light level, the high humidity level, the higher snow cover, the low number of branches due to self-pruning, and the high number of branches without bark may limit the growth and establishment of lichens. For instance, *Bryoria* are particularly vulnerable to long periods of hydration, and they have high decomposition rates under the snow cover (Goward, 1998; Campbell and Coxson, 2001; Coxson and Curteanu, 2002).

1.7 Conclusion

Our results showed that forest stands that have reached intermediate successional stages (between 101 and 200 years) contain a higher biomass of epiphytic lichens (*Bryoria* and *Usnea*) compared with younger (50–100 years) and older (>200 years) stages. Because our study did not focus on particular species but rather on species groups and because there may be other organisms or other lichen species that are associated with the older forest stages (>200 years), the conclusions of this study should be interpreted with caution. Indeed, within the same genus, some species may require different environmental conditions. For instance, in the same study area, Boudreault *et al.* (2002) showed that *B. furcellata* tends to be more abundant in younger forests.

Partial cuts that maintain or emulate structural characteristics of old forests should be used in lieu of even-aged silvicultural systems if the priority is to maintain a high epiphytic lichen biomass. It is also the safest way to maintain the reservoir of epiphytic lichen diversity. Particular attention should be paid to the preservation of old (101–150 years) and large trees (>16 cm DBH), as our results demonstrate that they are most important for lichen communities. The creation of canopy gaps by partial cuts could also increase penetration of light and humidity and favour lichen growth. However, canopy gaps that are too large could have the opposite effect (chapter 4).

When even-aged silvicultural systems are used, which is likely to remain the case in most of the Canadian boreal forest, the retention of large and old trees in regenerating areas, especially where these are maintained in small patches that buffer microclimate, will favour recolonization of young trees and maintain epiphytic lichen diversity. At the landscape level, because the different forest stages are likely to contain different species assemblages, it is essential to preserve a certain abundance of all forest successional stages in the regional forest mosaic. For the epiphytic lichen groups in this study, the protection of a significant proportion of postfire stands aged between 101 and 200 years should be prioritized because they contain a higher epiphytic biomass and because they are the most intensively exploited by the forest industry due to their high wood volume (Simard *et al.*, 2007).

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1.9 Tables

Table 1.1 Mean (± SD) of stand, tree, and branch characteristics for each age class, diameter at breast height (DBH) class, and height class

	Stem density (no./ha)		Basal area (m^2/ha)		Tree height (m)		Tree age (year)		Number of branches		Branch length (cm)	
	n	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD
Age classes (years)												
50-100	3	2758.3 ± 426.0a	3	41.5 ± 6.7a	34	13.7 ± 2.0a	35	67.1 ± 9.8c	36	185.5 ± 95.2a	36	70.5 ± 33.3a
100-150	3	2433.3 ± 711.2ab	3	32.8 ± 3.3ab	36	13.2 ± 2.4a	36	124.1 ± 6.5b	36	130.3 ± 54.4b	36	68.7 ± 33.5a
150-200	3	1441.7 ± 677.5bc	3	25.1 ± 5.8b	34	14.4 ± 2.9a	36	160.9 ± 19.8a	36	116.8 ± 45.1b	36	74.0± 38.8a
>200	3	1350.0 ± 114.6c	3	21.0 ± 3.9b	35	13.0 ± 2.7a	35	175.5 ± 39.0a	36	119.3 ± 58.2b	35	68.8 ± 38.3a
DBH classes (cm)												
8-12					39	11.1 ± 2.3c	39	123.9 ± 51.3b	40	98.2 ± 46.5c	39	66.7 ± 35.1b
12-16					45	13.3 ± 1.6b	47	133.5 ± 41.8ab	47	121.7 ± 48.8b	47	65.7 ± 31.6b
16-20					34	15.1 ± 1.7a	36	135.0 ± 50.5a	36	178.5 ± 74.8a	36	74.8 ± 38.6a
>20					21	16.2 ± 1.4a	21	139.3 ± 47.3a	21	174.7 ± 93.6a	21	76.5 ± 37.8a
Height classes (m)												
0-5									141	28.1 ± 24.6c	140	71.6 ± 38.0a
5-10									142	65.1 ± 32.1a	142	75.5 ± 30.9a
10-15									115	53.6 ± 33.7b	115	59.6 ± 16.0b

Note: Means with different letters differed significantly ($p \leq 0.05$) according to least squares means Tukey honest significant difference tests.

Table 1.2 Spearman rank correlations between variables measured at the tree level (n = 144)

	Tree height	Tree age	Tree DBH	No. of branches per tree
Tree height	-	0.116	0.756***	0.324***
Tree age		-	0.174*	-0.286***
Tree DBH			-	0.425***
No. of branches per tree				-

Note: Correlations with asteriks are significant at ***, $p < 0.001$; * $p < 0.05$).

Table 1.3 Two-way ANOVAs summary for the effects of age class (age) and tree diameter at breast height (DBH) on tree age (n = 143), tree height (n = 139), and number of branches (n = 144)

	Tree age			Tree height			No. of branches		
	df	F	p	df	F	p	df	F	p
Age	3, 8.1	39.82	**<0.001**	3, 8.4	1.10	0.402	3, 8.2	9.04	**<0.001**
DBH	3, 120	2.94	**0.036**	3, 118	56.43	**0.001**	3, 123	23.46	**<0.001**
Age x DBH	9,120	0.10	0.999	9, 118	2.50	**0.012**	9, 123	3.42	**0.001**

Note: Significant p values are given in boldface. The random effects site (age class) and tree (site x age-class x DBH class) were tested with the likelihood ratio statistic. The likelihood values for tree age, tree height, and number of branches were 46.7 ($p < 0.05$), 6.4 ($p < 0.05$), and 5.1 ($p < 0.05$), respectively.

Table 1.4 Nested two-way ANOVAs summary for the effects of age classes (age) and tree diameter at breast height (DBH) on biomass per branch of *Bryoria* ($n = 812$), *Evernia* ($n = 812$), and *Usnea* ($n = 816$) and on branch length ($n = 828$)

	Bryoria			*Evernia*			*Usnea*			Branch length		
	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Age	3, 7.7	5.62	**0.024**	3, 8.4	0.32	0.813	3, 7.8	4.35	**0.044**	3, 8.7	0.71	0.573
DBH	3, 121	4.51	**0.005**	3, 122	9.8	**<0.000**	3, 113	3.83	**0.012**	3, 113	5.22	**0.002**
Age x DBH	9, 118	1.11	0.356	9, 120	0.57	0.823	9, 110	0.37	0.946	9, 111	1.75	0.086

Note: Significant *p* values are given in boldface. The random effects site (age class) and tree (site x age class x DBH class) were tested with the likelihood ratio statistic. The likelihood values for the random effect site (age class) for *Bryoria*, *Evernia*, *Usnea*, and branch length were 63.1 ($p < 0.05$), 24.5 ($p < 0.05$), 7.2 ($p < 0.05$), and 3.2 ($p > 0.05$), respectively. The likelihood values for the random effect tree (site x DBH class x age class) for *Bryoria*, *Evernia*, *Usnea*, and branch length were 55.2 ($p < 0.05$), 3.4 ($p > 0.05$), 1.5 ($p > 0.05$), and 5.8 ($p < 0.05$), respectively.

Table 1.5 Nested two-way ANOVAs summary for the effects of age classes (age) and tree diameter at breast height (DBH) on biomass per tree of *Bryoria*, *Evernia*, and *Usnea* (n = 144)

	Bryoria				*Evernia*				*Usnea*			
	df		*F*	*p*	df		*F*	*p*	df		*F*	*p*
Age	3	8.4	6.85	**0.012**	3	8.1	0.21	0.884	3	8.2	2.60	0.123
DBH	3	122	24.09	**<0.000**	3	121	29.13	**<0.000**	3	122	19.98	**<0.000**
Age x DBH	9	122	0.51	0.862	9	121	0.46	0.897	9	122	0.68	0.728

Note: Significant p values are given in boldface. The random effect site (age class) was tested with the likelihood ratio statistic. The likelihood values for *Bryoria*, *Evernia*, and *Usnea* were 12.5 ($p < 0.05$), 40.0 ($p < 0.05$), and 16.4 ($p < 0.05$), respectively.

Table 1.6 Biomass per hectare of *Bryoria*, *Evernia*, and *Usnea* for each age class

	Biomass (kg/ha)					
	50-100 years	101-150 years	151-200 years	>200 years	*F*	*p*
Bryoria	52.1 ± 23.5b	216.3 ± 304a	174.6 ± 40.2a	89.4 ± 16.6b	20.36	**<0.001**
Evernia	14.2 ± 6.3a	16.0 ± 2.6a	9.3 ± 2.3ab	6.7 ± 1.4b	4.11	**0.049**
Usnea	1.2 ± 0.6b	4.9 ± 0.9a	4.1 ± 0.9a	1.1 ± 0.1b	24.53	**<0.001**

Note: Biomass values are means ± SDs. Significant *p* values are given in boldface. One-way ANOVAs were used to compare means between different age classes. Means with different letters differed significantly ($p \leq 0.05$) according to least square means Tukey's honestly significant difference tests.

1.10 Figures

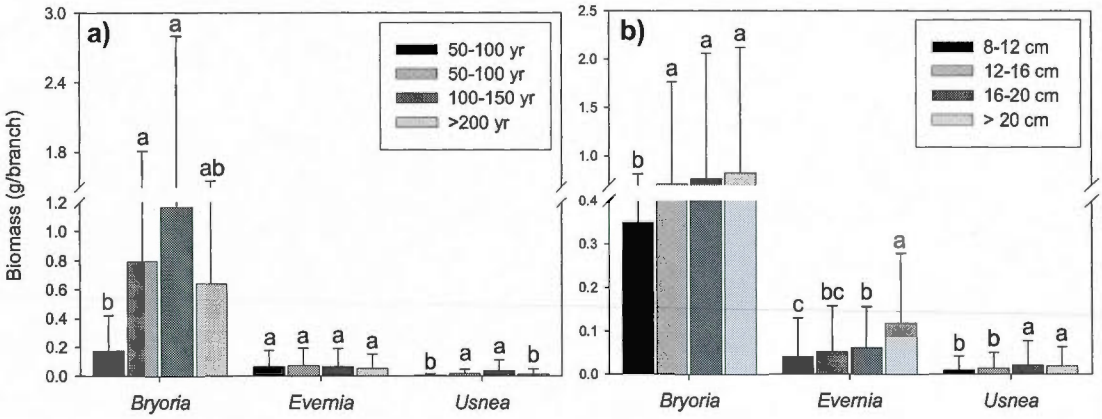

Figure 1.1 Biomass of *Bryoria* (n = 812), *Evernia* (n = 812), and *Usnea* (n = 816) at the branch level by age class (a) and diameter at breast height (DBH) class (b). Bars are means of untransformed data, and error bars are SDs. Nested two-way ANOVAs were used to compare means among different age classes and DBH classes. Means with different letters differed significantly ($p \leq 0.05$) according to least squares means Tukey's honestly significant difference tests.

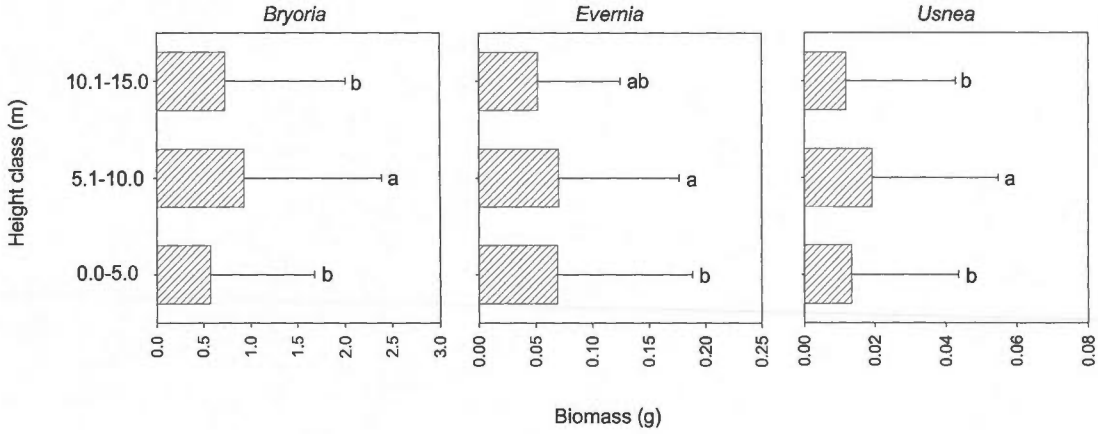

Figure 1.2 Biomass of *Bryoria*, *Evernia*, and *Usnea* at the branch level by height class. Bars are means of untransformed data, and error bars are SDs (n = 397). One-way ANOVAs were used to compare means among different height classes. Means with different letters differed significantly ($p \leq 0.05$) according to least squares means Tukey's honestly significant difference tests.

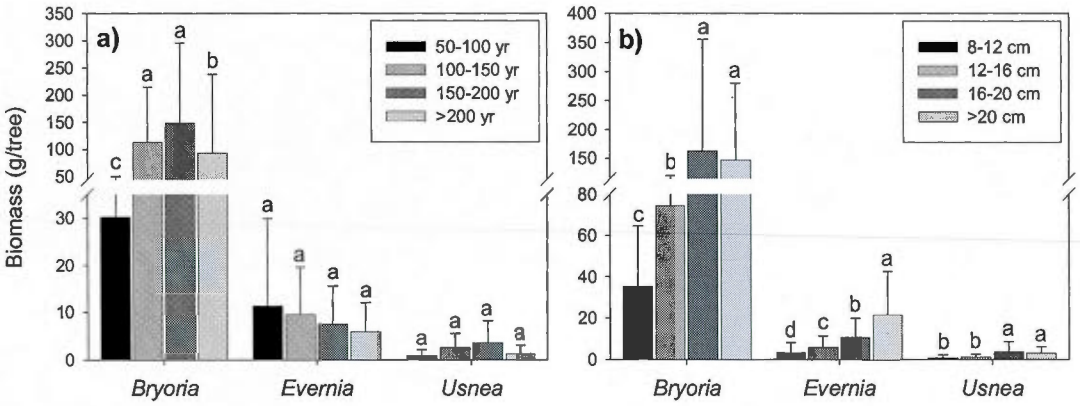

Figure 1.3 Biomass of *Bryoria*, *Evernia*, and *Usnea* at the tree level by age class (a) and diameter at breast height (DBH) class (b). Data are means of untransformed data, and error bars are SDs (n = 144). Nested two-way ANOVAs were used to compare means between different age classes and DBH classes. Means with different letters differed significantly ($p \leq 0.05$) according to least squares means Tukey's honestly significant difference tests.

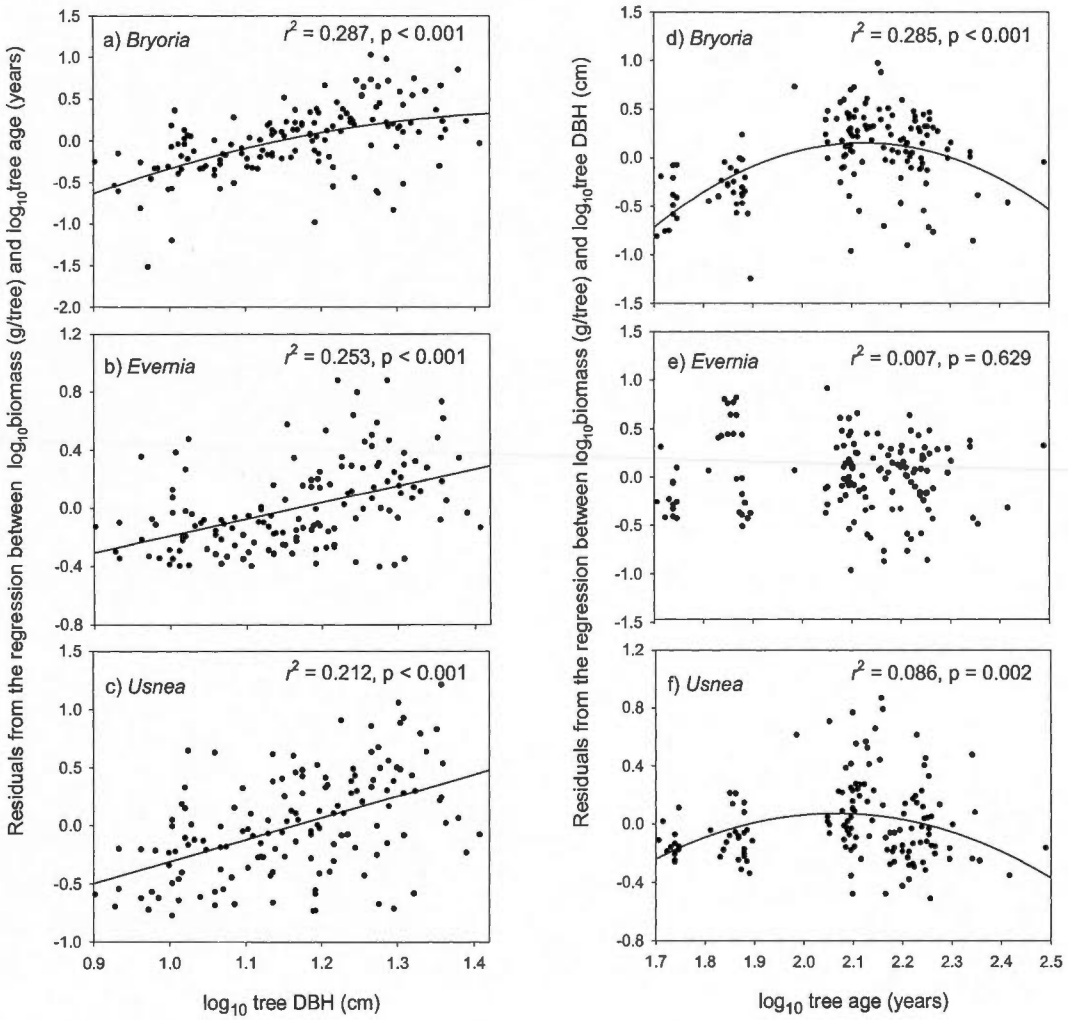

Figure 1.4 Regressions of residuals from the regressions conducted between biomass and tree age for *Bryoria* (a), *Evernia* (b), and *Usnea* (c) versus tree diameter at breast height (DBH) and of residuals from the regressions conducted between biomass and tree DBH for *Bryoria* (d), *Evernia* (e), and *Usnea* (f) versus tree age. Lines are shown only for significant relationships (n = 144).

1.11 Appendix

Appendix 1.1 Mean tree age and stand age of the chronosequence studied sites

Site	Age class (year)	Mean tree age (year)	Oldest tree (year)	Stand age (year)
N4	50-100	54.6 ± 1.5	57	57
N23	50-100	76.3 ± 1.3	91	91
S1	50-100	69.3 ± 6.1	92	92
N8	100-150	125.9 ± 8.5	131	131
N18	100-150	122.1 ± 5.5	131	131
n75	100-150	124.2 ± 5.1	132	132
C150	150-200	165.6 ± 4.7	167	167
POP	150-200	174.7 ± 5.3	180	180
FT6B	150-200	142.5 ± 21.7	180	180
L22	>200	168.3 ± 28.2	275	>200
N50	>200	156.7 ± 22.6	222	355
N6	>200	200.0 ± 50.6	280	710

CHAPITRE II

EDGE EFFECTS ON EPIPHYTIC LICHENS IN REMNANT STANDS OF MANAGED LANDSCAPES IN THE EASTERN BOREAL FOREST OF CANADA

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2.1 Résumé

Dans les paysages forestiers aménagés du Québec (Est du Canada), les corridors formés par les bandes riveraines et les séparateurs de coupe sont souvent parmis les seules forêts résiduelles productives qui demeurent présentes suite à une coupe. En raison de leur forme étroite, les effets de lisière sur la structure forestière et les lichens épiphytes peuvent s'avérer proportionnellement plus accentués dans ces fragments linéaires que dans des forêts résiduelles de forme plus compacte. Dans cette étude, nous avons comparé la biomasse totale de différents groupes de lichens épiphytes (*Bryoria* spp., *Usnea* spp., and *Evernia mesomorpha*) dans quatre différents types de forêts : séparateurs de coupe linéaires, bandes riveraines, grandes parcelles de forêts résiduelles et forêts d'intérieur. Nous avons aussi examiné si les effets de lisière sur la biomasse lichénique étaient présents dans deux types différents de forêts résiduelles, soit les séparateurs linéaires et les grandes parcelles de forêts résiduelles. Les lichens épiphytes ont été échantillonnés le long d'un transect perpendiculaire à la lisière de la coupe dans 10 réplicats pour chaque type de forêts. Nous avons utilisé des ANCOVA nichées pour comparer la biomasse lichénique en fonction des différentes distances et des types de forêts. La biomasse de *Bryoria* était plus élevée dans les grandes parcelles résiduelles et dans les forêts d'intérieur par rapport aux bandes riveraines et aux séparateurs de coupe, et la biomasse d'*Evernia* était plus élevée dans les bandes riveraines que dans les autres types de forêts. La biomasse d'*Usnea* ne variait pas selon les types de forêts. Le long des transects, la biomasse de *Bryoria* à 0 et 15 m à l'intérieur de la lisière était significativement plus basse qu'à 30 m. La biomasse d'*Evernia* et d'*Usnea* était significativement plus basse à la lisière de la coupe totale (0 m) comparativement aux parcelles localisées à l'intérieur (30 m). Nos résultats suggèrent que dans un paysage où seuls des séparateurs de coupe et des bandes riveraines seraient laissés en guise de forêts résiduelles, les communautés de lichens épiphytes typiques des forêts d'intérieur pourraient ne pas se maintenir, particulièrement les biomasses élevées de *Bryoria* observées dans les forêts d'intérieur. Des séparateurs de coupe plus larges pourraient être requis pour maintenir des conditions d'habitat d'intérieur pour les espèces associées aux forêts de stades successionnels avancés.

2.2 Abstract

In the managed boreal landscapes of Quebec (eastern Canada), corridors of riparian buffers and cut-block separators are often the only remnants of productive mature and overmature forests left in the harvested landscape. Because corridors are narrow and have multiple edges, edge effects on forest structure and on epiphytic lichens may be proportionally stronger in these linear remnant habitats than in more patch-like forest remnants. In this study, we compared the overall biomass of different epiphytic lichen taxa (*Bryoria* spp., *Usnea* spp., and *Evernia mesomorpha*) in four different forest types (linear cutblock separators, riparian buffers, large forest remnants, and control interior forests). We also examined whether edge effects on lichen biomass were present in two types of forest remnants (linear cutblock separators and large forest remnants). Epiphytic lichens were sampled along one transect perpendicular to clear-cut edge in 10 sites within each forest type. We used nested ANCOVA to compare lichen biomass among distance from edge classes and remnant forest types. *Bryoria* biomass was higher in large forest remnants and interior forests than in riparian buffers and cutblock separators, whereas *Evernia* biomass was higher in riparian buffers than in other forest types. *Usnea* biomass did not vary among forest types. On a transect into the forest, *Bryoria* biomass at 0 and 15 m from the edge was significantly lower than at 30 m. The biomass of *Evernia* and *Usnea* was significantly lower at the edge of the clear-cut (0 m) compared to interior plots (30 m). Our results suggest that a landscape where only cutblock separators and riparian buffers are left as remnant mature and overmature forests will not maintain epiphytic lichen communities of mature and overmature interior forests anywhere in the landscape, especially the high biomass of *Bryoria* observed in interior forests. Wider cutblock separators would be required to maintain core habitat conditions for species associated with late seral stages.

2.3 Introduction

Landscape fragmentation is of major concern for the conservation of biodiversity in forested landscapes. Habitat fragmentation is defined as the conversion of a formerly continuous habitat into small and isolated remnant patches (Meffe and Carroll, 1994), which results in the creation of biologically relevant edge effects (Donovan *et al.*, 1997, Esseen and Renhorn, 1998; Franklin and Forman, 1987; Sillett, 1994). At the edge between two units with high structural contrast, a forested zone where the microclimatic conditions are modified from the closed forest is often observed (e.g., increased amounts of sunlight, higher wind speeds, and larger fluctuations in temperature and humidity (Chen et al., 1993, Matlack, 1993). The proportion of habitats in this edge zone is related to the shape and size of the remnant fragment; for example, small and linear fragments have proportionally more edge than large and round fragments (Saunders *et al.*, 1991). The presence of an edge zone leads to a decrease in core habitat size (Öhman and Eriksson, 1998), thus making species associated with core habitats particularly impacted by edge effects, as their habitat area is reduced (Meffe and Carroll, 1994; Saunders *et al.*, 1991).

An increased rate of tree mortality due to windthrow is a major consequence of edge effects (Esseen, 1994; Jönsson *et al.*, 2007). Trees along the edges are more susceptible to uprooting or breakage of their bole or branches than trees found within a stand (Dewalle, 1983). The loss of dominant trees from the canopy can lead to serious modifications of forest structure and the light environment, and may alter species composition of communities (Saunders *et al.*, 1991). As clear-cut stands that are adjacent to remnant forests regenerate, edge effects usually decrease (Harper *et al.*, 2005); however, in some cases effects are still detected long after edge creation (Matlack, 1993; Rheault *et al.*, 2003).

Many studies report that epiphytic lichens are affected by edge effects (Belinchón *et al.*, 2007; Esseen, 2006; Esseen and Renhorn, 1998; Hilmo and Holien, 2002; Kivistö and Kuusinen, 2000; Rheault *et al.*, 2003; Sillett, 1994). Lichens are exposed to new levels of light, humidity, and wind after edge creation. Epiphytic lichens may be particularly sensitive to microclimatic modifications, because their metabolic activity varies passively with

environmental conditions (poikilohydric organisms) (Nash, 1996), particularly with the availability of light and water (Campbell and Coxson, 2001). For instance, shade-adapted species such as *Lobaria oregana* and *Pseudocyphellaria rainierensis* in Douglas–fir forests (Sillett 1994), and *Lobaria pulmonaria* in deciduous stands (Gauslaa and Solhaug, 1996) were affected by light intensity increases at the forest edge. Other studies have shown that fruticose lichens (pendant growth form) accumulate less biomass at forest edges (Esseen and Renhorn, 1998; Rheault *et al.*, 2003) and are prone to fragmentation by wind (Esseen, 1985), which is particularly relevant as they are the dominant epiphyte in boreal forests. A decline in available substrates (i.e., number of trees, number of branches per tree, and branch length) due to wind damage (Saunders *et al.*, 1991) may also explain the decrease in epiphytic biomass at the edge of forest remnants (Rheault *et al.*, 2003).

In the managed boreal landscapes of Quebec (eastern Canada), corridors of riparian buffer strips and upland strips are often the only remnants of productive mature and overmature forests left in the harvested landscape. Riparian buffer strips are widely used to minimize the impacts of logging on riparian habitats, which are key habitats for the maintenance of biodiversity and for ecosystem processes at the landscape level (Lamb *et al.*, 2003; Naiman *et al.*, 1993). Recently, upland strips (cutblock separators) were implemented in Quebec in order to reduce the maximum size of two adjacent cutblocks (Gouvernement du Québec, 2011). These linear habitats may act as refugia in harvested landscapes for species associated with mature and old-growth forest. By linking unharvested forest patches to one another, such corridors may also increase the probability of survival of local populations by promoting movement of individuals among patches (Bennett, 1990, 2003). In contrast, because corridors have multiple edges, edge influences on forest structure may be stronger in these linear remnant habitats than in patchy forest remnants (Mascarúa López *et al.*, 2006).

As linear habitats may act as biodiversity reservoirs in boreal forests, it becomes critical to evaluate the capacity of these corridors to maintain the integrity of communities of sessile organisms, such as lichens. Research efforts regarding sessile organisms have been mainly conducted in riparian buffers (e.g., Hylander *et al.*, 2002, 2005; Lamb *et al.* 2003), while the effectiveness of upland strips in maintaining the integrity of these organisms has been under-studied (but see Rheault *et al.*, 2003). In the current study, we address three questions: (1) are

there differences in the biomass of fruticose lichens (*Bryoria* spp., *Usnea* spp., and *Evernia mesomorpha*) between forest types (cutblock separators, riparian buffers, large forest remnants adjacent to a single clear-cut, and interior forests), (2) are edge effects present in cutblock separators and large forest remnants, and (3) are edge effects stronger in narrow linear corridors (cutblock separators) compared to large patchy forest remnants?

2.4 Methods

2.4.1 Study area

The study was conducted in the western part of the bioclimatic domain of the *Picea mariana*-feather moss forest in Quebec (49°00'–49°45' N, 76°00'–77°30' W) (Saucier and Robitaille, 1998). The area was located in the eastern part of the Abitibi region, near the municipality of Lebel-sur-Quévillon. This region forms part of the northern Clay Belt (Rowe, 1972), a broad physiographic unit characterized by lacustrine deposits from proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). Clay soils predominate, the topography is relatively flat, and the forest mosaic is dominated by black spruce (*P. mariana*) stands. Black spruce is occasionally interspersed with balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and eastern larch (*Larix laricina*). Jack pine stands dominate drier sites such as outwash deposits, old beaches, and eskers (Rowe, 1972). Clear-cuts adjacent to remnant forests were dominated by either naturally regenerated or planted black spruce or jack pine 1- and 5-m tall. From 1971 to 2001, a mean annual temperature of −0.7 °C and a mean annual precipitation of 905 mm were recorded at Matagami, located at approximately 100 km from our study sites (Environment Canada, 2004).

Mechanized-industrial logging, mainly clearcutting, began in the early 1970s. Since 1996, the Quebec government forest regulations require that clear-cuts do not exceed 150 ha (Gouvernement du Québec, 2005), and that between two contiguous cut-overs, cutblock separators dominated by trees >7 m in height must be retained. The width of the separators varies with the size of adjacent clear-cut areas. When adjacent clear-cuts are smaller than 100 ha, the width of cutblock separators is 60 m. If the size of one of the adjacent clear-cut areas

is over 100 ha, the width of the separator must be at least 100 m wide. The trees in the separators may be cut when the regenerating trees in the cut block reach 3 m. The riparian banks on both sides of permanent streams, lakes, or other surface water bodies must be protected by riparian buffers with a minimum width of 20 m on each side.

2.4.2 Lichen species in the study

We studied fruticose epiphytic lichens because they are the dominant epiphytic group in boreal forests. The three genera of fruticose lichens that we studied are *Bryoria*, *Usnea*, and *Evernia*, the only taxa of fruticose lichens present in the study sites. The most common and abundant *Bryoria* and *Usnea* species in our study area were *B. trichodes* ssp. *trichodes* and *U. filipendula*. *B. nadvornikiana*, *B. furcellata*, *B. lanestris*, *U. hirta*, and *U. subfloridana* were also frequently observed (unpublished data). Although present in the study area, *U. longissima* was encountered infrequently. *Evenia mesomorpha* is the only species of the genus that was present in our study area. Finally, *Hypogymnia physodes*, *Tuckermannopsis americana*, *Parmeliopsis ambigua*, *P. hyperopta*, *Mycoblastus sanguinarius*, and *Japewia tornoensis* were common epiphytic lichens in the forest stands that we sampled.

2.4.3 Sampling design

We studied epiphytic lichens in four types of forest: (1) 60 m wide cutblock separators; (2) 45–70 m wide riparian buffers surrounding streams; (3) large forest remnant patches adjacent to a single clear-cut that was at least 300 m wide; and (4) interior forests. Site selection was based on information gathered from digital forest inventory maps. Emphasis was placed on stands that were dominated by black spruce over 12 m in height and between 70 and 120 years of age. Edges between the remnants and the clear-cuts were straight. The sites were located near young edges that were between 5 and 11 years old, as this period was considered long enough to accumulate logging generated forest structure changes along edges (Ruel et al., 2001). Because available stands that fulfilled our criteria were limited, we did not control for edge orientation, although we recognize the importance of this factor (see Hylander, 2005). We preferred to maximize the number of stands within each forest type (riparian buffers, cutblock separators, large patches, and interior forests) to better understand within-forest type variability.

For each type of forest, we sampled 10 sites, for a total of 40 sites. In each site, we sampled epiphytic lichens along one transect perpendicular to the clear-cut edge. In cutblock separators the transects crossed the separators from side to side (60 m), in large forest remnants the transects went 60 m into the forest, and in riparian buffers the transects varied between 45 and 75 m in length due to the variability in buffer width. In interior forests, epiphytic lichens were collected along 100-m long transects located near the large forest remnant transects, but deeper within the same forest stand; they were located at least 100 m away from any edge. Large forest remnants, cutblock separators, and interior forests were chosen in a way to maximize similarity in soil features, slope, and tree species composition. None of these three forest types contained riparian habitats.

Epiphytic lichens were sampled in rectangular plots of 5 m × 20 m (long axis parallel to the forest edge) located at 15-m intervals along each transect in the cutblock separators, riparian buffers, and in the large forest remnants. Interior forests were sampled with three plots spaced 50 m apart from one another along transects. Data on forest structure variables were collected in the plots. All live trees, standing dead trees (snags), and fallen trees (logs) ≥ 5 cm DBH (diameter at breast-height) were inventoried. Only logs with intact bark (classes 1 and 2, Thomas *et al.*, 1979) were sampled, because the objective was to detect forest damage due to recent harvesting (for more detail, see Mascarúa López *et al.*, 2006). In each plot, we randomly selected 10 black spruce trees. For each tree, we sampled one branch (length >100 cm) at a randomly selected height (between 1.5 and 5 m) and orientation. We then measured the branch length and branch width and we assessed its vitality (dead/live). The distal 100 cm of these branches were pruned and the branch diameter at the cutting point was measured. Branches were brought back to the laboratory and we sorted thalli of *E. mesomorpha*, *Bryoria* spp., and *Usnea* spp. Lichens were dried at 60 °C for 24 h before being weighed (0.0000 g).

2.4.4 Data analyses

Simple linear regression was used to detect significant relationships between tree and branch characteristics (independent variables), and lichen biomass (dependent variables) for the three taxa on branches collected across all forest types. Variables selected were branch length,

branch diameter, tree DBH, stem density and basal area. Regressions were conducted with mean values calculated at the plot level.

Differences in epiphytic lichen biomass among forest types (i.e., cutblock separators, riparian buffers, large forest remnants, and interior forests; $n = 40$) were tested at the transect level (calculated over all sampled branches in each transect) by using one-way ANOVA (PROC GLM, SAS Institute 2002). Forest type was the main effect. Stand (stem density, basal area, mortality, and windthrow) and branch characteristics (branch diameter, branch length, and proportion of live branches) were also compared among forest types with one-way ANOVA. Mortality was calculated as the ratio of logs plus snags to the number of all trees (live and dead), and windthrow was calculated as the ratio of logs to the number of all trees (live and dead) that were recorded in each transect. The response variables were mean lichen biomass and branch characteristics calculated over all sampled branches in each transect. Stand structure variables were estimated by averaging all plots in each transect. Biomass data were square-root transformed ($x^{0.5} + (x + 1)^{0.5}$), branch length data were log-transformed ($\log x$), and mortality and windthrow data were arcsine-transformed ($\text{arcsine}(x/100)^{0.5}$) to conform to the normality and homoscedasticity assumptions of ANOVA. We used post hoc Tukey HSD tests to detect significant differences ($p \leq 0.05$) among forest types. Chi-squared tests were used to compare lichen frequencies between forest types for the three taxa. Pearson chi-square components ($\chi 2$: $[O - E]^2/E$) were used to measure the difference between observed (O) and expected (E) values. The response variables were presence or absence of the taxa on each collected branch.

Nested two-way ANCOVA models were used to compare lichen biomass and stand and branch characteristics among distance classes (for the first 30 m) and remnant forest types. Forest type (cutblock separators and large forest remnants) and distance from the edge (0, 15, and 30 m) were fixed factors, sampling site was a random factor nested within the forest type, and stem density and stand age were added as covariates in the analyses (except for variables of stand structure). Nested ANOVA was used to account for site variability within-forest type. Analyses were performed with the MIXED procedure of SAS (SAS Institute, 2002). Response variables were mean lichen biomass and mean branch characteristics calculated over the 10 branches that were collected in each 5 m × 20 m plot, and stand characteristics for

each 5 m × 20 m plot. Since cutblock separators had two plots for some distances (i.e., the transects crossed their entire width), these plots were averaged prior to the analyses. Biomass data were square-root transformed ($x^{0.5} + (x + 1)^{0.5}$), branch length data were log-transformed (log x), and mortality and windthrow data were arcsine-transformed (arcsine$(x/100)^{0.5}$) to fulfill basic assumptions of parametric procedures. Denominator degrees-of-freedom were calculated using Satterthwaite's approximation (Littell *et al.*, 1996). Since the MIXED procedure does not compute an F-test for the variance component of random effects, the significance of the random effect was calculated with the likelihood ratio statistic, which was computed by taking the difference between the −2 REML log-likelihood (Restricted Maximum Likelihood estimator) of the model containing the random effect and the model without the random effect, as suggested by Littell *et al.* (1996). Significant differences ($p \leq 0.05$) between distance and forest type classes were detected with Tukey HSD tests. No attempt was made to evaluate edge effects in riparian buffers because edge effects in this forest type are a combination of a natural gradient changing with increasing distance to the water and an anthropogenic gradient at the edge of the clear-cut; thus, it is difficult to detect edge effects in this type of habitat without an appropriate control of riparian habitats imbedded within continuous forests.

The importance of edge aspect on lichen biomass in cutblock separator transects was also assessed. As all linear cutblocks separators had similar orientation, the difference between their south-south-east (SSE) and north-north-west (NNW) facing edge plots (0 m from the edge) was tested with one-way ANOVA. Response variables were mean lichen biomass calculated over the 10 sampled branches collected within a plot. Lichen biomass values were square-root transformed. No attempt was made to evaluate the edge aspect in large forest patches because most of them were SSE-oriented (7 out of 10).

2.5 Results

2.5.1 Relationships between lichen biomass and stand and branch characteristics

Branch length was significantly correlated with branch diameter ($r = 0.438$, $p < 0.001$). The biomass of *Bryoria* increased significantly with branch diameter and branch length, but r^2

values are low, indicating relatively weak relationships (Fig. 2.1). The biomass of *Evernia* and *Usnea* was unrelated to any branch characteristics ($p > 0.05$). Live branches had 3.8 times more biomass of *Bryoria* than dead ones, but approximately the same amount of *Usnea* and *Evernia*. No significant relationship between stand variables (tree DBH, basal area, and stem density) and lichen biomass was found (results not presented).

2.5.2 Comparison among forest types

Basal area was significantly lower, and mortality and windthrow were significantly higher in cutblock separators compared to interior forests (Table 2.1). Branches were significantly shorter in riparian buffers compared to large forest remnants. Stem density, branch diameter, and number of live branches did not differ among forest types (Table 2.1).

Species of the genus *Bryoria* dominated lower tree canopies in interior forests. *Bryoria* was almost 8 times more abundant than *Usnea* and 30 times more abundant than *Evernia* (Fig. 2.2). *Usnea* was four times more abundant than *Evernia* (Fig. 2.2). *Bryoria* was also the most frequent taxon: it occurred on all sampled branch sections. In cutblock separators and in large forest remnants, *Bryoria* was again much more abundant in terms of biomass than *Usnea* and *Evernia*, but in riparian buffers, its biomass was only twice that of *Usnea* and *Evernia* (Fig. 2.2). *Usnea* and *Evernia* had a similar biomass in cutblock separators and in riparian buffers, but the biomass of *Usnea* was higher than that of *Evernia* in large forest remnants.

Bryoria biomass was significantly lower in cutblock separators and in riparian buffers than in interior forests and large forest remnants (Fig. 2.2; $F_{3,36} = 13.09$, $p < 0.001$). *Evernia* biomass was significantly greater in riparian buffers than in other forest types (Fig. 2.2; $F_{3,36} = 8.45$, $p < 0.001$), and *Usnea* biomass did not differ significantly across the different forest types (Fig. 2.2; $F_{3,36} = 1.32$, $p = 0.282$). There were no significant differences between large forest remnants and interior forests for these three lichen taxa (Fig. 2.2).

Evernia was more frequently found on branches in riparian buffers (60.2%) compared to cutblock separators (54.7%), interior forests (48.6%) and large forest remnants (42.5%) ($\chi 2 = 26.43$, $p < 0.001$). *Usnea* was less frequent in cutblock separators (66.2%) than in large forest remnants (76.8%), riparian buffers (78.6%), and interior forests (78.8%) ($\chi 2 = 19.38$, $p <$

0.001). *Bryoria* was frequent in all forest types (>95%), but its frequency in interior forests (99.8%) was significantly higher ($\chi 2 = 10.89$, $p = 0.012$).

2.5.3 Influence of distance from forest edge

Basal area, stem density, mortality, windthrow, and branch diameter differed significantly with distance to forest edge, but not between cutblock separators and large forest remnants (forest type) (Table 2.2 and Table 2.3). At the edge, stem density and basal area were lower, and windthrow and mortality was higher than at 30 m, but the differences between 0 and 15 m were not significant for stem density and windthrow (Tukey HSD tests; Fig. 2.3). Branches had a smaller diameter at 0 and 15 m from the edge than at 30 m (Tukey HSD tests; Fig. 2.3). The interaction term was not significant for any stand or branch variables, whereas site variability was significant for all variables except branch diameter (Table 2.2 and Table 2.3).

After taking into account the influence of stand age and stem density, the difference in lichen biomass among distance classes was significant for *Bryoria* and *Usnea* and nearly significant for *Evernia* ($p = 0.055$) (Table 2.3). Lichen biomass differed significantly among remnant forest types for *Bryoria* and *Evernia*, and among sites for *Evernia* and *Usnea* (Table 2.3). Since the interaction term was not significant for *Bryoria*, *Evernia*, or *Usnea* (Table 2.3), the effect of distance was consistent across forest types. *Bryoria* biomass was significantly greater in large forest remnants than in cutblock separators, whereas the reverse was found for *Evernia* (Tukey HSD tests). *Bryoria* biomass at 0 and 15 m was significantly lower compared to 30 m (Tukey HSD tests), and was 2.3 times higher in large forest remnants than in cutblock separators (Fig. 2.4). *Usnea* biomass at 0 m was half of that at 30 m, whereas biomass at 15 m was not significantly different from those at 0 and 30 m (Tukey HSD tests). *Evernia* biomass was smaller at the edge compared to that at 30 m (Tukey HSD tests), and the mean value at the edge of cutblock separators was 3.6 larger than at the edge of large forest remnants (Fig. 2.4).

The magnitude of edge influence computed as the ratio between edge and interior values in cutblock separators and large forest remnants for *Bryoria* was, respectively, 0.38 and 0.57, for *Usnea* 0.32 and 0.51, and for *Evernia* 0.59 and 0.29.

No significant effect of edge aspect in cutblock separators was detected with ANOVA for *Bryoria* ($F_{1,16} = 1.99$, $p = 0.180$), *Evernia* ($F_{1,16} = 2.93$, $p = 0.106$), or *Usnea* ($F_{1,16} = 1.69$, $p = 0.212$).

2.6 Discussion

2.6.1 Comparisons among forest types

In theory, larger remnants support larger populations and have a bigger core area unaffected by edge effects than smaller remnants (Saunders *et al.*, 1991). In this study, *Bryoria* biomass at the transect level was similar in large forest remnants and interior forests, but biomass was much lower in the relatively small cutblock separators. This pattern suggests that large forest patches are better habitats for *Bryoria* than cutblock separators. The overall higher biomass of *Bryoria* in large forest remnants compared to cutblock separators may also be an effect of continuous immigration of lichens from forest interiors (source populations) in large forest remnants. In fact, large forest remnants were situated in the edges of interior forests, while the distances between interior forests and cutblock separators were much larger. Differences between large forest remnants and cutblock separators that are likely related to edge effects are discussed in more detail in Section 4.2.

Riparian buffers were characterized by a relatively high biomass of *Evernia* and a relatively low biomass of *Bryoria.* In general, riparian zones are characterized by a naturally open forest structure with trees adapted to a greater penetration of light and wind stress, which results in the root stimulation necessary to develop root stability (Mitchell, 1995). For the same study sites, Mascarúa López *et al.* (2006) found that the edge influence on forest structure was lower in riparian buffers compared to cutblock separators and that stem density near streams was low even if little damage (mortality or windthrow) was observed. It is likely that the species composition of lichen epiphyte communities in the riparian zone is adapted to light, wind, and microhabitat conditions of the pre-existing edge near a stream. *E. mesomorpha* is a frequent and abundant species in sites exposed to full sunlight (Brodo *et al.*, 2001), which may explain its high biomass in riparian forests. In contrast, fragmentation of

lichen thalli or high light intensity in these open forests might have been too high to promote *Bryoria* biomass accumulation.

2.6.2 Edge influence

Edge effects on biomass per branch were detected for all lichen taxa and in both types of forest edge (cutblock separators and large forest remnants). However, the distance and the magnitude (ratio between edge and interior values) of edge influence vary with taxa and forest type. The distance of edge influence toward the forest interior was greater for *Bryoria*, the dominant group of lichens, than for *Usnea* and *Evernia*; however, the magnitude of edge effect was similar for *Usnea* and *Bryoria*. We documented stronger edge effects on *Bryoria* in cutblock separators, which are exposed to two close anthropogenic edges, than for large forest remnants, exposed to only one edge. For instance, edge and mid-distance *Bryoria* biomass values were less than half the ones found in large forest remnants. Similarly, Mascarúa López *et al.* (2006) found that distance of edge influence on forest structure extends 10–25 m from the clear-cut edge into large forest remnants, and across the entire width of cutblock separators. These results align with the general theory that predicts that long and narrow habitats are more affected by edge effects than larger habitats with a more regular shape (Saunders *et al.*, 1991). Multiple edges seem to increase the magnitude and extent of edge effects (Fletcher, 2005; Mascarúa López *et al.*, 2006). In this study, the core area of interior conditions for *Bryoria* in 60-m wide cutblock separators was considerably reduced: at least 50% of these habitats were affected by edge effects.

Biomass accumulation of epiphytic lichens depends on successful colonization of propagules (dispersal and establishment) and subsequent growth and fragmentation of lichen thalli. Edge effects can affect any of these different processes. Moreover, substrate characteristics are important for lichen establishment (Armstrong, 1990). In our study, the lower biomass of *Bryoria*, *Usnea*, and *Evernia* at the edge of forest remnants may reflect the lower quality of substrates at forest edge. For instance, at the edges of clear-cuts and remnant forests, branches had a smaller diameter. Our results and those of other studies (e.g., Esseen *et al.*, 1996) showed that lichen biomass increased with branch diameter. For tree species that have a bark with a tendency to exfoliate, thalli may be entirely dislodged from the branches during

windy conditions. The establishment success of diaspores on branches may also be diminished by windy conditions at the edge, as suggested by Hilmo and Holien (2002) to explain the low number of juvenile thalli of *Bryoria* spp. found at forest edges in spruce stands in Norway. Substrate losses by windthrow at the edge of remnant forests will directly affect the biomass of epiphytic lichens found in remnant stands, but it will also have an indirect effect by decreasing the amount of propagules present in forests for subsequent colonization (Hilmo and Holien, 2002).

Lichen growth under relatively closed forest canopies may be limited because lichen photosynthesis is rarely at its maximum rate at low light level (Esseen, 2006; Green *et al.*, 1995). Higher light levels following edge creation and windthrows may thus favor the growth of lichen thalli. For instance, Esseen and Renhorn (1998) proposed that the increase in biomass of *Alectoria sarmentosa* observed 11–16 years after logging at mid-distance from the edge was a result of an increase in light intensity. Similarly, higher growth rates of two foliose lichens (*L. pulmonaria* and *Platismatia glauca*) were found at 12 m from the edge (Renhorn *et al.*, 1997). In our study, there is a trend for increased abundance at mid-distance from the edge in large forest remnants but this was not significant (see Fig. 2.4). It is possible that the growth rate of at least some thalli might have increased after edge creation; but the growth of species more frequent and abundant in dense and closed canopy forests, such as *B. nadvornikiana* (Brodo and Hawksworth, 1977, Brodo *et al.*, 2001), may be adversely affected by new forest conditions following edge creation. An ongoing study showed that canopy opening following partial cutting has negative impacts on the growth of *B. nadvornikiana* in the western part of the boreal forest of Quebec (chapter 4). Furthermore, increased evaporation at edges may lead to shorter hydration event time and thus reduce the time for photosynthetic activity as suggested by Esseen (2006). The effect of environmental modifications might be particularly pronounced for small thalli (Gauslaa and Solhaug, 1998), as proposed for *Bryoria* spp. by Hilmo and Holien (2002), because they may desiccate more rapidly than large ones.

Epiphytic lichens only accumulate biomass if growth rates are superior to thallus fragmentation rates. The lower biomass of *Bryoria* in cutblock separators and riparian buffers and the significant decrease in biomass of *Bryoria*, *Usnea*, and *Evernia* at the edge of

cutblock separators and large forest remnants suggest that fragmentation could have eliminated the positive effects due to increased light levels induced by edge creation. Although thallus fragmentation is an efficient and natural way of dispersal for many *Bryoria* species (Dettki, 1998; Esseen, 1985; Stevenson, 1988), thalli are not adapted to strong winds since they developed in relatively closed stands (Esseen and Renhorn, 1998). Thus, strong winds can have a negative impact on lichen biomass accumulation by causing excessive thallus fragmentation at forest edges (Esseen and Renhorn, 1998; Rheault *et al.*, 2003). Thalli that have subpendant or pendant growth form and filamentous species with highly dissected thalli, like *B. trichodes* and *B. nadvornikiana*, can be easily fragmented by wind (Esseen, 1985). High lichen mortality is mainly associated with extreme climatic events such as storms, particularly during autumn and winter, or heavy snow load on branches (Esseen, 1985). However, species of *Bryoria* that grow rolled up around branches such as *B. furcellata* would be less affected by thallus fragmentation (Rheault *et al.*, 2003). In managed landscapes of northwestern Québec, Rheault *et al.* (2003) suggested that the dominance of *B. furcellata* in their study may explain the weak influence of edges on the biomass of this species of *Bryoria*. The presence of a central axis in *Usnea* (Esseen, 1985; Renhorn, 1997) and the robustness of *E. mesomorpha* thalli make these species (except for *U. longissima*) less prone to fragmentation compared with *Bryoria*, and may explain the lower edge influence found for *Usnea* and *Evernia* in our study.

Edge effects on poikilohydric organisms can vary according to edge aspect (Kivistö and Kuusinen, 2000; Hylander, 2005). For instance, Hylander *et al.* (2005) showed that exposure to sunlight between north-north-east and south-south-west facing edges modify the growth of two mosses at the edge. On the other hand, Renhorn *et al.* (1997) found no influence of edge aspect on the growth rates of *L. pulmonaria* and *P. glauca*, but in this case, only one east facing edge was investigated. East aspect might represent the most favorable edge for epiphytic lichens, with intermediate light levels and a moister microclimate (Chen *et al.*, 1993). No difference in lichen biomass between SSE and NNW facing edges of cutblock separators was detected in our study. Since the study was not designed specifically to address this question, it is impossible to determine precisely whether this is due to an absence of

effect, or to multiple effects that cancel each other (thalli fragmentation due to wind exposure, desiccation due to solar radiation, etc.).

2.6.3 Management implications

Epiphytic lichens are more abundant in mature and old-growth forests than in regenerating forests because biomass accumulation is a slow process that occurs as the forests age (Dettki and Esseen, 1998; Esseen *et al.*, 1996; Lesica *et al.*, 1991; McCune, 1993). Consequently, in landscapes harvested by clear-cuts, epiphytic lichens are mainly restricted to remnant habitats of mature and old forests. Because these remnants are mostly of linear shape in black spruce forests, edge effects become an important component particularly in cutblock separators that are likely to experience changes in the composition of the lichen communities.

Since lichens were not identified at the species level, it is not possible to tell if some species are more affected by edge effects than others. Hence, conclusions at species level may eventually differ from those at genus level. However, our results suggest that a managed forest where the only mature and overmature stands remaining are cutblock separators and riparian buffers will not maintain the integrity of epiphytic lichen communities at the landscape scale, notably the high biomass of *Bryoria* observed in interior forests. Such a management approach is also likely to jeopardize lichen recolonization of regenerating areas, lichen metapopulation dynamics (Snäll *et al.*, 2005), and other organisms that are associated with epiphytic lichens such as invertebrates and forest birds (Pettersson *et al.*, 1995).

Within a managed forest, some measures must be adopted to reduce edge effects by diminishing the contrast between remnant habitats and the regenerating matrix (Esseen, 2006), while increasing connectivity between remnant habitats and favor epiphytic lichens recolonization. For upland corridors such as cutblock separators our results reemphasize Mascarúa López *et al.* (2006) conclusions that 60 m wide strips are not large enough to maintain core habitat conditions for species associated to late seral stages. Therefore, the width of linear habitats should be increased. Partial cuts could be used at the interface between clear-cuts and remnant forests to compensate for the economic losses associated with the widening of corridors, while decreasing the risk of windthrow, increasing the size of

the core habitats, and generating a more gradual transition between edge and interior conditions. For instance, Stevenson and Coxson (2008) found that green-tree retention in cutblocks adjacent to remnant forest patches significantly reduces edge effects on sensitive old-growth canopy lichens (i.e. *Lobaria retigera*). Because the decrease in edge effects over time is dependent on the trees in regenerating areas, it is also important to insure that regenerating areas near edges are well stocked. Riparian buffers might be adequate for maintaining epiphytic lichen communities living at the interface of aquatic and terrestrial ecosystems since little damage to forest structure was detected by Mascarúa López *et al.* (2006). However, further research that compares continuous forests with a riparian zone to riparian buffers are needed to evaluate edge effects in this type of habitat.

Finally, because biomass accumulation of epiphytic lichens is a slow process that requires forest continuity, forest management units should contain large tracts of mature and overmature forests between cutover areas that offer adequate interior conditions and few edge effects. Even if cutblock separators and riparian buffers could not maintain by themselves the integrity of interior mature or overmature forest epiphytic lichen community in a forestry-dominated landscape, they could act as "life-boats" by providing refuge for lichen species and increase connectivity between large tracks of residual forests. When large forests are linked with linear and patchy remnant habitats in cutover landscapes, they could be functional "source" habitats in a context of metapopulation dynamics (Sillett *et al.*, 2000). Consequently, to preserve their functional roles in managed landscapes, cutblock separators should be maintained in cutover landscapes.

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2.8 Tables

Table 2.1 Mean ± S.E. of stand and branch characteristics among forest types[a], together with F-statistics and p-values from one-way ANOVAs used on forest types ($n = 40$)

Characteristic	Cutblock separators	Riparian buffers	Large forest remnants	Interior forests	$F_{3,36}$	p
Basal area (m^2/ha)	15.5 ± 2.1 b	22.3 ± 2.2 ab	23.2 ± 1.5 ab	25.0 ± 2.7 a	**3.58**	**0.023**
Stand density (stems/ha)	1076.7 ± 143.7 a	1457.8 ± 195.2 a	1324.5 ± 170.1 a	1730.0 ± 194.7 a	2.36	0.088
Mortality (%)	37.3 ± 4.9 a	22.6 ± 3.2 ab	31.7 ± 4.6 ab	21.3 ± 3.6 b	**3.48**	**0.026**
Windthrow (%)	12.0 ± 3.2 a	7.5 ± 2.2 ab	8.6 ± 3.7 ab	2.6 ± 1.0 b	**2.92**	**0.047**
Branch diameter (mm)	11.1 ± 0.3 a	10.3 ± 0.4 a	11.6 ± 0.2 a	10.9 ± 0.4 a	2.27	0.097
Branch length (cm)	117.3 ± 3.4 ab	109.1 ± 4.6 b	127.8 ± 5.9 a	113.3 ± 4.6 ab	**2.91**	**0.048**
Live branches (%)	22.0 ± 4.3a	14.7 ± 3.1a	24.3 ± 3.7a	22.5 ± 4.2	0.54	0.656

Note: Significant effects ($p \leq 0.05$) are shown in bold type. Within each row, means with different letters differ significantly according to least squares means Tukey's honestly significant difference tests.

[a] Means were calculated with three distance classes for cutblock separators, riparian buffers, and interior forests and with five distance classes in large forest remnants.

Table 2.2 Nested ANCOVA summaries for effects of forest type (large forest remnants and cutblock separators) and distance from the edge (three distance classes in each forest type: 0, 15 and 30 m) on stand characteristics ($n = 60$)

Source	d.f	Basal area (m^2/ha)		Stem density (stems/ha)		Mortality (%)		Windthrow (%)	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Forest type	1	2.34	0.143	1.45	0.244	0.49	0.492	0.01	0.924
Distance	2	**8.85**	**<0.001**	**7.44**	**0.002**	**6.79**	**0.003**	**4.34**	**0.028**
Forest type × distance	2	0.54	0.586	0.81	0.453	2.3	0.115	2.01	0.161

Note: Significant effects ($p \leq 0.05$) are shown in bold type. The random effect site (forest type) was tested with the likelihood ratio statistic. The likelihood values for stem density, basal area, mortality, and windthrow were, respectively, 10.5, $p < 0.05$; 20.4, $p < 0.05$; 19.1, $p < 0.05$; and 9.4, $p < 0.05$.

Table 2.3 Nested ANCOVA summaries for effects of forest type (large forest remnants and cutblock separators) and distance from the edge (three distance classes in each forest type: 0, 15 and 30 m) on biomass of *Bryoria*, *Evernia*, and *Usnea*, and branch characteristics ($n = 56$)

Source	d.f.	Branch length (cm)		Branch diameter (mm)		Live branches (%)		*Bryoria* (g)		*Evernia* (g)		*Usnea* (g)	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Forest type	1	1.67	0.214	0.01	0.917	0.03	0.855	**6.55**	**0.021**	**5.62**	**0.030**	0.32	0.582
Distance	2	1.53	0.232	**4.55**	**0.017**	0.54	0.589	**4.39**	**0.020**	3.15	0.055	**3.59**	**0.039**
Forest type × distance	2	0.29	0.751	0.41	0.667	0.46	0.633	0.03	0.973	0.65	0.530	0.18	0.835
Stem density	1	4.01	0.052	0.34	0.564	1.86	0.181	0.10	0.751	0.11	0.745	0.37	0.546
Stand age	1	0.20	0.658	1.43	0.250	0.24	0.629	1.21	0.289	1.62	0.222	1.16	0.301

Note: Significant effects ($p \leq 0.05$) are shown in bold type. Stem density and stand age were treated as covariates and site was nested within-forest type (random factor). The random effect site (forest type) was tested with the likelihood ratio statistic. The likelihood values for *Bryoria*, *Evernia*, *Usnea*, branch length, branch diameter, and proportion of live branches were, respectively, 3.0, $p > 0.05$; 4.5, $p < 0.05$; 4.1, $p < 0.05$; 5.9, $p < 0.05$; 1.3, $p > 0.05$; and 7.1, $p < 0.05$.

2.9 Figures

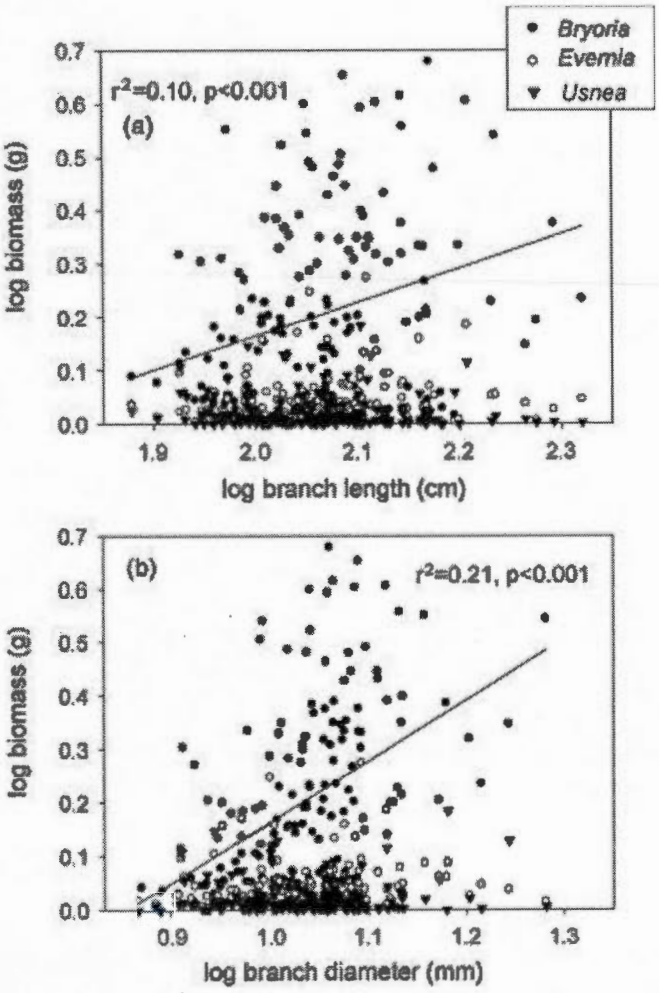

Figure 2.1 Relationships between lichen biomass and branch characteristics: (a) branch length (*Bryoria* spp.: $r^2 = 0.10$, $p < 0.001$; *Evernia mesomorpha*: $r^2 = 0.02$, $p = 0.06$; *Usnea* spp.: $r^2 = 0.001$, $p = 0.68$) and (b) branch diameter (*Bryoria* spp.: $r^2 = 0.21$, $p < 0.001$; *E. mesomorpha*: $r^2 = 0.006$, $p = 0.30$; *Usnea* spp.: $r^2 = 0.02$, $p = 0.08$) ($n = 167$). Lines are shown only for significant relationships.

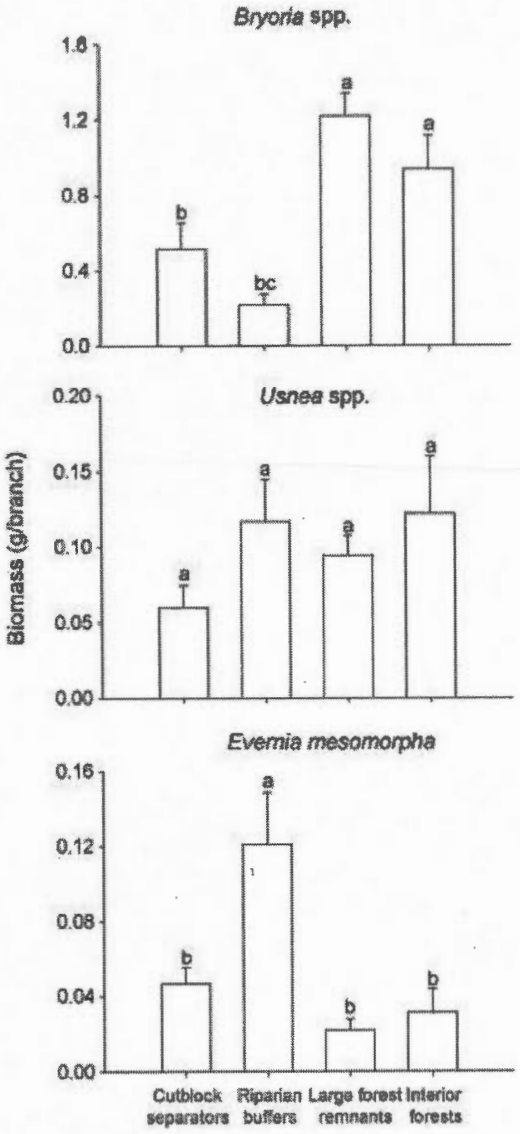

Figure 2.2 Comparison of biomass (mean ± S.E.) among forest types (cutblock separators, riparian buffers, large forest remnants with only one edge, and interior forests) for *Bryoria* spp., *Usnea* spp., and *Evernia mesomorpha*. Means with different letters differed significantly ($p \leq 0.05$) based on LSmeans Tukey HSD tests. Means were calculated with three distance classes for cutblock separators, riparian buffers, and interior forests and with five distance classes in large forest remnants. Note that scales are different in each graph.

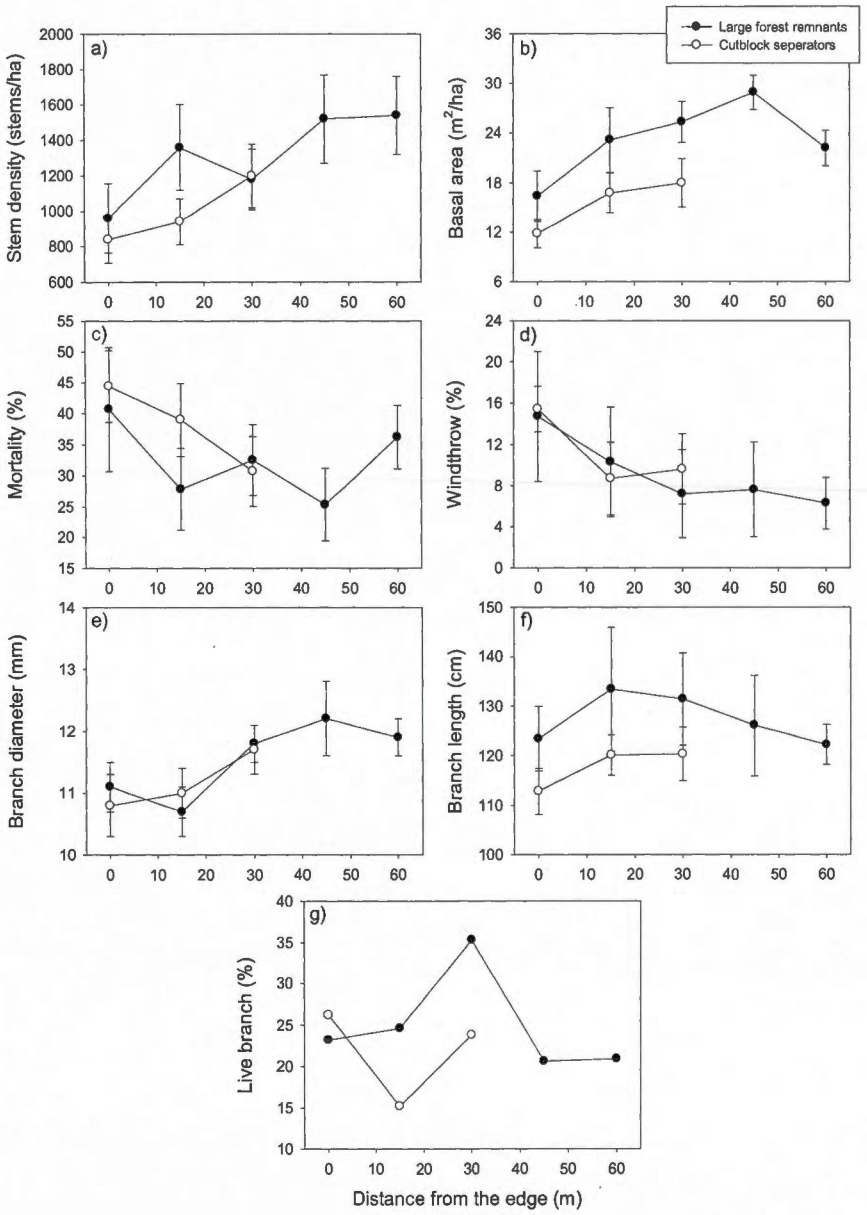

Figure 2.3 Mean values ± S.E. of stand and branch characteristics along the clear-cut edge-to-interior gradient in cutblock separators (0 m: n = 10; 15 m: n = 9; 30 m: n = 10) and in large forest remnants (0 m: n = 8; 15 m: n = 9; 30 m: n = 10; 45 m: n = 10; 60 m: n = 10): (a) stem density, (b) basal area, (c) mortality, (d) windthrow, (e) branch diameter, (f) branch length, and (g) proportion of live branches. Data from the two clear-cut edges were combined for cutblock separators.

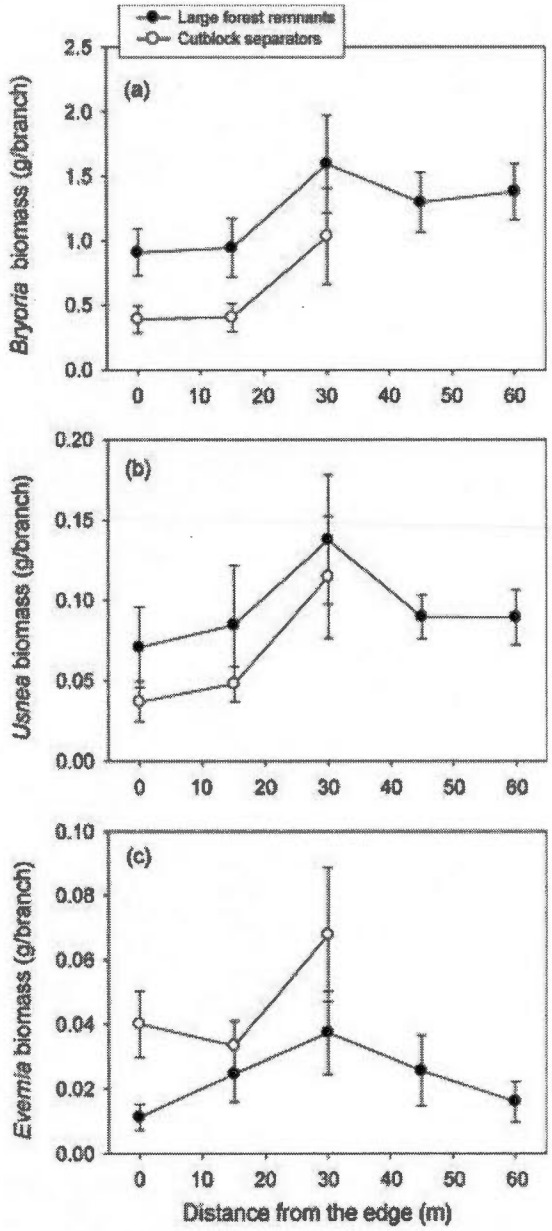

Figure 2.4 Mean values ± S.E. of lichen biomass along the clear-cut edge-to-interior gradient in cutblock separators (0 m: $n = 10$; 15 m: $n = 9$; 30 m: $n = 10$), and in large forest remnants (0 m: $n = 8$; 15 m: $n = 9$; 30 m: $n = 10$; 45 m: $n = 10$; 60 m: $n = 10$): (a) *Bryoria* spp., (b) *Usnea* spp., and (c) *Evernia mesomorpha*. Data from the two clear-cut edges were combined for cutblock separators.

CHAPITRE III

EPIPHYTIC LICHEN COLONIZATION IN REGENERATING BLACK SPRUCE FOREST STANDS

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3.1 Résumé

La colonisation des jeunes peuplements par les lichens épiphytes est un phénomène important pour le maintien de populations viables dans les paysages forestiers affectés périodiquement par les perturbations sévères. Nous avons examiné la colonisation de différentes espèces relativement communes de lichens foliacés et fruticuleux épiphytes dans des peuplements d'épinette noire en régénération dans la forêt boréale de l'ouest du Québec. Le nombre de thalles ainsi que l'abondance des espèces ont été mesurés sur des branches prélevées sur des jeunes arbres localisés dans des coupes totales, à différentes distances de forêts matures adjacentes (de 5 m à 100 m). Nous avons échantillonné des peuplements régénérés de deux façons, soit des peuplements issus d'une régénération naturelle qui s'est établie en sous-étage avant la coupe totale, et des peuplements régénérés par plantation suite à la coupe. Les lichens ont aussi été inventoriés dans deux classes d'âge de coupes, soit des coupes âgées de 6 à 12 ans et des coupes âgées de 12 à 18 ans. Les résultats indiquent que pour les coupes récentes, le nombre de thalles et l'abondance par branche étaient supérieurs dans les peuplements issus de régénération naturelle pour la plupart des espèces de lichens épiphytes, alors que cette différence entre les deux types de régénération s'estompait dans les peuplements plus âgés. La distance par rapport au peuplement adjacent exerçait peu d'influence sur l'abondance des thalles pour la plupart des espèces, sauf pour celles qui se dispersent principalement par fragments de thalles, et particulièrement *Bryoria* spp., pour lesquelles le nombre de thalles était significativement plus élevé à 5 m qu'à 100 m. Ces résultats suggèrent donc que la plupart des espèces de lichens parviennent à coloniser les microsites présents dans les peuplements en régénération, peu importe l'origine de cette régénération. En discussion nous soulignons toutefois que ce résultat doit être mis en perspective, puisque la matrice forestière dans la région à l'étude contient toujours une forte proportion de peuplements vierges matures, et que les sources de propagules (et les taux de colonisation) pourraient décliner au fur et à mesure que ces vieux peuplements sont récoltés et remplacés par des peuplements plus jeunes.

3.2 Abstract

Colonization of young forest stands by epiphytic lichens is an important phenomenon for the maintenance of viable populations in forest landscapes affected by periodic severe disturbances. We examined colonization of relatively common fruticulose and foliose epiphytic species in regenerating black spruce stands in boreal forests of western Québec. The number of thalli as well as the abundance of each species were measured on branches sampled on young trees located in recently harvested stands, at different distances from adjacent mature forests (from 5 m to 100 m). We sampled stands that were regenerated with two methods: stands that regenerated using advance regeneration that established in the understory before harvest, and stands that were regenerated with post-harvest plantations. Lichens were also inventoried in two age classes in terms of time elapsed since harvesting, namely between 6 and 10 years and between 12 and 18 years. The results indicate that for the younger age class, the number of thalli as well as the abundance of branches was superior in stands regenerated using advance regeneration for most epiphytic lichen species, whereas the difference between the two types of regeneration disappeared in the older age class. Distance from the adjacent stand had little influence on thalli abundance for most species, except for those that disperse mainly through thallus fragments, particularly *Bryoria* spp., for which the number of thalli was significantly higher at 5 m than at 100 m. These results suggest that most lichen species can colonize the microsites present in regenerating stands, independently from regeneration type. However, we underline that this result should be put in perspective, because the forest matrix in the studied region still contains an high proportion of virgin mature stands, and that propagule sources (and colonization rates) could decline as these mature stands continue to be harvested and replaced by younger stands.

3.3 Introduction

In landscapes that are fragmented by forest management activities, interruption of the connectivity between forest habitats can hamper species dispersal and colonization among forest remnants, and could also have repercussions on the recolonization of recently disturbed areas (Kupfer *et al.*, 2006; Lindenmayer and Franklin, 2002). In boreal forests, many important differences exist between the two main disturbances, forest harvesting and fire, that could affect propagule availability. For example, at the landscape scale, forest management causes a decrease of the proportion of old forests (Bergeron *et al.*, 2002), and can result in vast expanses of regenerating forests (Jetté *et al.*, 2008). These large areas of regenerating forests containing few mature forest remnants contrast with fires that generally leave a proportion of forest remnants that were either spared by the fire or only partially burned (Kafka *et al.*, 2001; Leduc *et al.*, 2000). Residual forests left after clearcutting are often either unproductive (Bergeron *et al.*, 2002), or very small in size with linear shapes (Boudreault *et al.*, 2008), which often accentuates the importance of edge effects which further diminish the amount of forest-interior habitats. At the stand scale, few residual living trees are generally left in stands following clearcut, which contrasts with the residual living trees left behind after natural disturbances (Harper *et al.*, 2004).

In Canadian boreal forests where clearcutting is a major disturbance factor, it is important to obtain basic knowledge on recolonization patterns of vulnerable organisms with limited dispersal capabilities in landscapes that have been fragmented by recent disturbances. Epiphytic lichens are a sensitive group in this respect: several studies show that species associated with relatively old forest habitats can also grow in young forests habitats, suggesting that they are dispersal limited (Hilmo and Såstad, 2001; Keon and Muir, 2002; Sillett *et al.*, 2000). These sensitive species may need a relatively long period of time to colonize a new forest stand. Other studies have shown that as distance from mature adjacent forests increases, lichen abundance on the branches of small regenerating trees (Dettki *et al.*, 2000; Stevenson, 1988) and the number of thallus fragments that dispersed from neighboring trees (Dettki, 1998) tend to decrease. These dispersal limitations could partly explain the

slow accumulation rates of epiphytic lichens in forest environments (Boudreault *et al.,* 2009; Dettki and Esseen, 1998; Esseen *et al.,* 1996; Hyvärinen *et al.,* 1992; Neitlich, 1993).

However, biotic factors other than dispersal capabilities could also influence species colonization in recently disturbed environments. After the arrival of a propagule in a new habitat, fixation to the substrate, propagule germination, initial development of the juvenile thallus, growth of the mature thallus, and reproduction are essential life stages (Armstrong, 1988; Hilmo and Såstad, 2001). Depending on circumstances, most of these life stages could be limiting for the colonization process. For example, rapid development of the hyphae that fix the lichen to the tree or branch substrate is crucial for lichen establishment (Hilmo and Såstad, 2001). Moreover, juvenile development of epiphytic species can be a slow process (Hyvärinen *et al.,* 1999), even for species that are abundant and opportunist (Hilmo and Ott, 2002). Factors such as substrate quality, substrate availability and microclimatic conditions also influence diaspore fixation on the substrate, diaspore survival, and thallus growth (Armstrong, 1988).

Lichens reproduce sexually through spore production by the fungal associate, or asexually through the production of symbiotic propagules, containing at the same time the mycobiont and the phycobiont (soredia, isidia, thallus fragments, etc.). Spores would probably be the best dispersal agents for long distance dispersal (Barkman, 1958; Hedenås *et al.,* 2003). Soredia and isidia allow lichen colonization on intermediate distances, and thallus fragments facilitate colonization on short distances (Barkman, 1958). According to Ahti (1977), asexual dispersal dominates in boreal forests.

For many fruticose species (*Alectoria* spp., *Bryoria* spp., *Usnea* spp.), thallus fragmentation plays an important role in epiphytic lichen dispersal (Stevenson 1985, 1988) on short distances or at the stand scale (Gauslaa *et al.*, 1997). Dispersal on longer distances for these species would be insured by spores or soredia (Gauslaa *et al.*, 1997). Fruticose lichens, especially those belonging to the *Bryoria* and *Usnea* genera, are dominant in mature and old forests of western Québec (Boudreault *et al.,* 2009).

In boreal forests, young stands that were regenerated following planting could represent ideal conditions to retrospectively study and quantify colonization from adjacent unlogged stands, because it is known that these young trees were initially devoid of epiphytic lichens. Moreover, by comparing epiphytic lichen communities on young planted trees with those on young trees that regenerated naturally in the understory (advance regeneration), it is also possible to evaluate the influence of silvicultural practices used to restock former clearcuts on the development of lichen communities. It is expected that because natural advance regeneration was exposed to propagule colonization from overstory trees before the cut, it would harbour richer lichen communities compared with planted trees. This type of information could be very useful for the conservation of epiphytic lichen communities in managed forest mosaics.

The objectives of this study were 1) to compare epiphytic lichen colonization in clearcut-origin stands that were regenerated naturally with stands regenerated through plantation, 2) to evaluate the influence of the time-since-harvesting on species colonization in the regenerating stands, and 3) to determine if epiphytic lichen abundance decreases with increasing distance from adjacent unlogged forests. Our hypotheses are: 1) that the colonization will be higher in stands that regenerated naturally, 2) that species colonization will increase with time since harvesting, and 3) that species whose main mode of dispersion is through fragments of thalli will be the most strongly affected by an increasing distance to the edge.

3.4 Methods

3.4.1 Study area

The study was conducted in Quebec's closed-crown boreal forest, more precisely in the western part of the *Picea mariana*-feathermoss bioclimatic domain (Saucier and Robitaille, 1998). The sampling sites (49°00' - 49°45' N, 76°00' - 77°30' W) were located in the eastern part of the Abitibi region, around the localities of Lebel-sur-Quévillon and Matagami. The topography of this region is relatively flat. Surficial deposits in this region are co-dominated by glacial tills, interspersed with lacustrine deposits originating from the proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). Forest composition on both kinds of

deposits is overwhelmingly dominated by black spruce stands (*Picea mariana*) (Rowe, 1972). Ground cover in closed-crown black spruce stands is generally dominated by *Pleurozium schreberri*. Over time, successional paludification generally takes place, meaning that *P. schreberri* is replaced by sphagnums, and that tree stem density and tree size drecrease (Simard *et al.*, 2009). The closest weather station is located in Matagami, where the annual mean temperature recorded during the 1970-2000 period was 0.7°C, and mean annual precipitation for the same period was 905 mm (Environment Canada, 2004).

Forest management activities have been taking place in this region since the early 1970's, coinciding with the initial development of road access in this remote region. Clearcutting is by far the most common harvesting method. Since the mid-1980's, forestry standards in the province of Québec demand that any advance regeneration present in the understory must be protected in stands that are to be harvested, and tree-planting is generally used only if such regeneration is absent. Natural advance regeneration in these stands is generally dominated by black spruce, and this species is also the one that is used the most often when planting is considered. Isolated mature veteran trees are sometimes left in clearcut areas, but they generally represent less than 5% of the original tree cover in a given stand, and in the context of this study were mostly represented by trees with diameter at breast-height < 10 cm.

3.4.2 Sampling design

We studied epiphytic lichen colonization along 34 transects established across clearcuts that were done between 1985 and 1999. The sampling was stratified according to (1) the regeneration type after cutting: stands that regenerated naturally with advance regeneration (19 transects) and plantations (15 transects), and (2) time since harvesting: young clearcuts (6-10 years) or old clearcuts (12-18 years). All transects were placed perpendicular to unlogged forest edges. In addition to this stratification, the following factors were considered during site selection: the transect had to be located perpendicular to straight edges that were at least 200 m in length, topography had to be flat, the regenerated stands and adjacent stands had to be > 4 ha in size, adjacent stands had to be mature or overmature (>90 years), the distance of the transects from the road had to be >100 m, adjacent stands had to be dominated by black spruce, and natural regeneration and plantations had to be dominated by black

spruce. Also, we made sure that the portion of the transect located farthest from the forest edge (100 m) was not located close to another edge located elsewhere around the clearcut area. Because the number of available stands that fulfilled all our criteria was limited, we did not control for edge orientation, although we recognize the importance of this factor for dispersal study.

We studied lichen colonization on black spruce branches collected in each transect in plots located at four distances from the forest edge: 5, 25, 50 and 100 m. The 10 regenerating black spruce trees that were located closest to the center of the plots were selected and the height and diameter at breast height (DBH) of each tree were measured. On each tree, two branches with length of at least 50 cm were selected. The branches were collected at random height (between 30 and 100 cm above ground) and orientation. The outermost 50 cm section of these branches was sampled and the branch diameter at the cutting point was measured. At each distance, inside a circular 40 m^2 plot, we also counted the number of regenerating trees (DBH > 1 cm at height of 1.3 m)

The sampled branches were brought back to the laboratory where the number of thalli (>1 mm) of each lichen species was counted on the upper portion of the main axis of each branch. The proportion of the upper portion of the main axis covered by each species was also estimated on each branch. We used standard chemical tests in lichenology (spot tests; see Brodo *et al.*, 2001) to identify small lichen thalli. *Bryoria* spp. and *Usnea* spp. were treated at the genus level. On one out of two branches, the age of the branch was evaluated by counting the number of foliar scars or, for larger branches, the number of growth rings.

3.4.3 Studied lichen species

This study focused on common species in the study area to avoid difficulties associated to juvenile thalli identification. Moreover, species belonging to the genera *Bryoria* and *Usnea*, which are common epiphytic species in this region, were not identified at the species level due to the difficulties associated with species-level identification of juvenile thalli. Knowing the dispersal mode of these main species or species groups is also important in order to interpret correctly the results of this study. The fruticose lichen species studied and their

principal mode of dispersal were: *Bryoria* spp. (soredia, thalli fragments), *Evernia mesomorpha* (soredia), and *Usnea* spp. (soredia, thalli fragments). The foliose lichen species and their principal mode of dispersal were: *Hypogymnia physodes* (soredia), *Imshaugia aleurites* (isidia), *Parmelia sulcata* (soredia), *Parmeliopsis ambigua* (soredia), *Parmeliopsis hyperopta* (soredia), *Tuckermannopsis americana* (spores), and *Vulpicida pinastri* (soredia).

3.4.4 Statistical analyses

Differences in number and DBH of regenerating trees, branch age, and branch diameter between regeneration types and time since harvesting classes were tested with mixed ANOVAs. Stand regeneration type (natural or plantation) and time since harvesting (young or old clearcuts) were considered fixed effects and sampling site nested within the interaction of regeneration type and time since harvesting was considered a random effect. The response variables were mean values of each variable calculated at the plot level ($n = 133$). Data were log transformed to satisfy the normality and homoscedasticity of ANOVA.

The number of thalli and the cover of each species or group of species (fruticose and foliose lichens) were analysed using mixed ANOVA models. Regeneration type, time since harvesting, and distance from the edge were fixed factors, sampling site was a random factor nested within the interaction of regeneration type and time since harvesting, and the interaction of sampling site and distance was nested within the interaction of regeneration type and time since harvesting. All interactions among the fixed effects were included in the model. Response variables were the number of thalli and the cover per branch for each lichen taxa. Data were log transformed ($\log x + 1$) to satisfy the normality and homoscedasticity of ANOVA for all variables except for *Usnea* spp., *E. mesomorpha* and *P. sulcata* that were rank transformed.

ANOVA analyses were performed with the MIXED procedure in SAS (SAS Institute, 2002). The random effects were used as error term when testing for differences between fixed effects. Significant differences ($p \leq 0.05$) between classes in all ANOVAs analyses were detected with LS means Tukey HSD tests.

Linear regressions were used to detect significant relationships between tree and branch characteristics (independent variables), and the number and the cover of fruticose and foliose lichens (dependent variables) for each regeneration type. The independant variables selected were number of regenerating trees, DBH of regenerating trees, branch age, and branch diameter. Regressions were based on mean values calculated at the plot level.

3.5 Results

3.5.1 Stand, tree, and branch characteristics

DBH of regenerating trees, branch diameter and branch age of regenerating trees were significantly higher in stands that regenerated naturally compared with plantations (Tables 3.1 and 3.2). Number, DBH, and height of regenerating trees were also significantly higher in old clearcuts than young clearcuts (Tables 3.1 and 3.2). In general, a significant interaction between the type of regeneration and time since harvesting indicate that most of these values were significantly lower in young plantations (Tables 3.1 and 3.2).

3.5.2 Overall lichen abundance in regenerating stands

Among fruticose lichen species, the *Bryoria* species group was the most abundant (in terms of number of thalli and cover), both in naturally regenerated stands and in plantations (Fig. 3.1). Among foliose lichen species, *P. ambigua* was the most abundant species (in terms of number of thalli and cover) in naturally regenerated stands, whereas *H. physodes* and *T. americana* were the most abundant species in plantations (Fig. 3.1). The number and cover of foliose lichen were higher than the number and the cover of fruticose lichens, both in naturally regenerated stands and in plantations.

3.5.3 Effects of regeneration type, time since harvesting, and distance from the remnant stand on the number of lichens in regenerated stands

Because few differences were observed between analyses based on the number of thalli or on lichen cover, only the results of the analyses performed on the number of thalli will be

presented in the following sub-sections (3.5.3, 3.5.4, and 3.5.5). The results of the analyses done on lichen cover data are presented in Appendices 3.1, 3.2, 3.3, and 3.4.

The number of thalli differed significantly between regeneration types for *I. aleurites*, *P. ambigua*, *P. hyperopta*, *V. pinastri*, fruticose lichens, and foliose lichens (Table 3.3), and was higher in naturally regenerated stands compared to plantations. For instance, foliose and fruticose lichens were 1.8 times and 2.3 times more numerous respectively in naturally regenerated stands compared to plantations. Time since harvesting had a significant effect, as a higher number of thalli was encountered in old clearcuts for *T. americana*, *H. physodes*, *P. sulcata*, and foliose lichens, whereas a higher number was encountered in young clearcuts for *I. aleurtites*. The effect of distance from adjacent forests was significant only for *Bryoria* spp.: the number of thalli was 1.5 times higher at 5 m comparatively to 100 m, but did not differ significantly from values observed at 25, and 50 m (Fig. 3.1). A significant interaction between regeneration type and time since harvesting was identified for all species and for foliose and fruticose lichens (Table 3.3 and Fig. 3.2), indicating that the effect of time since harvesting was inconsistent between regeneration types. Within naturally regenerated stands, significant differences between time since harvesting categories were observed for many species (*I. aleurites*, *P. ambigua*, *P. hyperopta*, and *V. pinastri*), all of which were more numerous in young clearcuts (Fig. 3.2). Conversely, when plantations are analysed separately, significant differences were observed between time since harvesting categories for several species and species groups (*Bryoria* spp., *E. mesomorpha*, *H. physodes*, *P. sulcata*, *Usnea*, *T. americana*, and foliose lichens), the number of thalli being higher in old plantations (Fig. 3.2). In general, branches of regenerating trees in older plantations had similar numbers of lichen thalli compared with older naturally regenerated stands, and some species were even more numerous in old plantations (*H. physodes*, *P. sulcata*, and *T. americana*) (Fig. 3.2).

3.5.4 Influence of branch, tree, and stand characteristics on the number of lichens in regenerating stands

The number of foliose and fruticose thalli increased significantly with branch age (Fig. 3.4a) and branch diameter (Fig. 3.4b) in both types of regeneration. Figure 3.4c shows an increase

in number of fruticose and foliose lichens with DBH of regenerating trees in plantations. Tree DBH was positively correlated with branch age in plantations ($r_{Spearman} = 0.650$, $p < 0.001$). No relationship between tree DBH and branch age was observed in naturally regenerated stands ($r_{Spearman} = 0.107$, $p = 0.366$). The number of thalli of foliose and fruticose species decreased significantly with the number of regenerating trees in naturally regenerated stands, but r^2 values are low, indicating relatively weak relationships (Fig. 3.4d). The number of foliose lichens increased significantly with the number of regenerating trees in plantations (Fig. 3.4d).

3.6 Discussion

The number of lichen thalli that establish on regenerating trees depends on the dispersal capabilities of each lichen species, and also from different factors influencing colonization, such as time elapsed since the stand-originating disturbance, the type of forest regeneration (natural advanced or planted), and tree and branch characteristics. The potential effects of these different factors, as well as the influence of the mode of reproduction of each lichen species on colonization success, will be discussed in the following sections.

3.6.1 Environmental factors influencing lichen colonization

Time elapsed since the stand-originating disturbance – Many studies have shown an increase in the accumulation of epiphytic lichens with stand age (Boudreault *et al.,* 2009; Esseen *et al.,* 1996; Hyvärinen *et al.,* 1992; Lesica *et al.,* 1991; Neitlich, 1993). Our results also indicate that the abundance of most lichen species generally respond positively to an increase in time available for branch colonization. Three reasons can be proposed to explain the increase in number of thalli and lichen cover with time. First, the branches were exposed during a longer period for lichen inoculation, thallus development and growth. Our results show such an increase in the number of lichen thalli and in lichen cover as a function of branch age (Fig. 3.4b and Appendix 3.4b). However, as opposed to what was expected, we did not observe a significant difference in lichen abundance between the young and old stands originating from advance natural regeneration. This result might be due in part to the absence of significant differences in branch age between the two age classes of naturally

regenerated stands (see Tables 3.1. and 3.2). However, branch age cannot explain in itself the variability in observed lichen thalli number and cover in regenerating stands, because fixed effects (regeneration type and time since harvesting) were still significant when branch age was added as a covariable in the statistical models (results not presented). Secondly, some stand, tree, or branch structural characteristics that facilitate lichen establishment and growth tend to vary according to time since disturbance; these factors will be discussed in the next section. Thirdly, epiphytic lichen colonization or development rates are relatively low in general. A relatively long period of dormancy is observed after the initial attachment of the diaspores on a tree branch substrate (Hilmo and Ott, 2002), and the appearance of the first lobules will take a relatively long time for many lichen species, for example 12, 21, and 24 months for *Lobaria pulmonaria* (Scheidegger, 1995), *L. scrobiculata*, and *Platismatia glauca* (Hilmo and Ott, 2002), respectively. Following this period, several years must elapse before the appearance of a mature thallus (Hilmo and Ott, 2002) and before many species can produce propagules, thus delaying the possibility of colonizing new habitats (Kalwij *et al.*, 2005; Scheidegger, 1995). According to Hilmo and Ott (2002), the low light availability, low temperatures, and the snow that covers the diaspores during winter also have for effect to shorten the duration of the growth period in boreal forests, and could explain that several years are needed for thallus development.

Regeneration type and stand characteristics – Results from our study indicate that young black spruce stands originating from advance regeneration contain a higher number of lichen thalli and a higher cover of epiphytic lichen species compared with young black spruce plantations. In stands dominated by advance regeneration, the young trees established from seed or layering before harvest, which is confirmed by the age of the sampled branches (see Table 3.2). This advance regeneration mechanism is commonly observed in coniferous stands in this region (Doucet, 1988). These young trees probably benefited from nearby epiphytic lichen propagule sources, such as the dominant canopy trees that were subsequently harvested (Peck and McCune, 1997; Sillett and Goslin, 1999). Even if small trees do not present optimal substrates for epiphytic lichen colonization (see Esseen *et al.*, 1996), these regenerating trees generally have branches that are older and larger than those on trees located in plantations.

For the older regenerating stands of natural or plantation origin, we observed that the advantages conferred by an inoculation prior to stand harvesting are no longer significant. A first explanation could be that planted trees could have more available microsites for lichen colonization than naturally regenerated trees, because they were initially devoid of lichens when they were planted, which could have favored a faster increase in lichen cover and number of individuals, as observed by Romagni and Cries (2000). Indeed, these authors observed a similar phenomenon when they compared lichen cover in sites that were severely and less severely burned: lichens located in severely burned habitats established faster due to lower competition levels. A second explanation could be that young stands present a hostile environment for thalli that remained on advance regeneration after harvesting. Thus the initially greater loading on naturally regenerated trees may largely be lost due to wind- and snow-scouring of branches, or from dieback beneath snow cover in the first decade after harvesting. Coxson and Coyle (2003) found that mechanical processes, especially wind scouring of thalli, were dominant in determining biomass accumulation of *Bryoria* in mature sub-boreal spruce forests, and were more important than establishment and growth rates in structuring community gradients. Thus, similarities in lichen number and cover between regeneration types that emerge between the older stand types do not necessarily imply a faster rate of colonization or reduced competition rates, but could merely imply higher mortality (or greater turnover) of thalli in younger naturally regenerated stands. This could also explain why, as opposed to our initial expectations, a higher number of thalli were often observed in young naturally regenerated clearcluts compared with old naturally regenerated clearcuts.

Adjacent forest stands and landscape context – The proportion of mature forests in the forest mosaic surrounding regenerating stands is another factor that could influence lichen colonization (Stevenson, 1988), but this factor was not measured in this study. In the context of Quebec's black spruce forests, where harvest history is still relatively recent, the forest landscapes are mostly constituted by former large tracts of undisturbed forests that were recently affected by a first cycle of forest harvesting. At the time of the study, a relatively important proportion of the remaining forests around the sampling sites were still relatively old virgin stands. This high proportion of old forests at the landscape scale may have

facilitated lichen colonization in regenerating areas after clearcut harvesting. However, in the years to come, the mature residual forests that were left beside the studied stands could be harvested when vegetation height in regenerating areas reaches a height of three meters or more (Gouvernement du Québec, 2011). Because the older clearcuts examined in this study have almost reached this height (see Table 3.2), adjacent mature stands could soon be harvested, which might decrease the availability of potential sources of propagules, both at the stand and landscape scales. Lichen abundance within residual stands could also be negatively affected by edge effects, a phenomenon that has been well described in the region (Boudreault *et al.*, 2008; Rhcault *et al.*, 2003). Boudreault *et al.* (2008) showed that lichen abundance in narrow habitats was half of that observed in large forest remnants. Consequently, it is likely that the colonization rates observed in this study do not reflect the colonization rates that could be observed in future harvested areas or that could have been observed if clearcuts studied had been located adjacent to narrow habitats.

3.6.2 Lichen reproduction mode

In general, dispersal distances mentioned in the literature for soredia and thalli fragments are relatively short. For example, the maximal dispersal distance reached by soredia of *Hypogymnia physodes* is 25 m (Armstrong, 1987), the mean and maximal distances reached by soredia of *L. pulmonaria* are respectively of 35 and 75 m (Öckinger *et al.,* 2004), and fragments of *U. longissima* generally reached a maximal distance of 5 m (Esseen, 1981). According to Dettki *et al.,* (1998), *Bryoria* species generally disperse relatively well comparatively with other alectorioid lichens (e.g., *Alectoria sarmentosa*), because they fragment more easily, and because they produce smaller and more numerous diaspores. According to Goward (2003), *Bryoria* species are not limited primarily by dispersal and their absence from regenerating forests in British Columbia are rather due to limitations in substrate availability in closed canopy forests. However, Stevenson and Coxson (2003) show a dramatic decline in the dispersal of *Bryoria* fragments at distance greater than 10 m from the forest edge. Dettki *et al.* (2000) and Stevenson (1988) show a reduction of about 50% in colonization rates at 100 m compared with sites immediately adjacent with residual forests.

Overall, distance from adjacent forests had little influence on lichen abundance in regenerating areas. This was particularly obvious for species that disperse by soredia, isidia or spores, for which 100 m probably does not represent a significant dispersal distance. Only the group formed by all *Bryoria* species combined, whose main mode of dispersal is by fragments of thalli, were significantly affected by distance from adjacent forests both in artificially and naturally regenerated areas. Our results indicate that the number of thalli and lichen cover are respectively 1.5 and 1.8 times lower at 100 m compared with number and cover at 5 m. These results confirm the hypothesis that species dispersed primarily by fragments of thalli have more limited dispersal capabilities compared with species having other modes of dispersal, and that particular attention should be devoted to these species considering their importance in black spruce forest ecosystems. Indeed, *Bryoria* spp. are the dominant species group in mature to old forests of this region (Boudreault *et al.,* 2009). *Usnea* species, which can also disperse by fragments, possess a central cord that probably make them more resistant to fragmentation compared with *Bryoria* species. According to Halonen *et al.* (1998), dispersal of *Usnea* is mostly insured by soredia which could confer to these species an advantage over *Bryoria* for long-distance dispersal. Our results contrast with Dettki *et al.* (2000) who found dispersal limitations in both sexually and asexually dispersed species, including those dispersed by soredia. It should be noted that the regenerating stands studied by Dettki *et al.* (2000) were considerably older than those in the present study, and that the landscape differed by having a longer history of forest harvesting.

This study was done in a region of the province of Quebec where the climate is relatively dry, and where some lichen species typically associated with relatively humid old-growth boreal forests are absent or seldom encountered (e.g., cyanolichens, *Alectoria sarmentosa*). Colonization capabilities of these species could respond differently to factors such as regeneration type, time since harvesting, or distance from nearest adjacent mature stand. For example, the dispersal capabilities of *A. sarmentosa* are known to be much lower than those of *Bryoria* (Dettki, 1998; Dettki *et al.*, 2000), and even if this species is absent from our study area, it can be quite abundant in other regions of the province (Arseneau *et al.*, 1997; Laflamme-Lévesque *et al.*, 1983).

3.7 Conclusion

This study showed that colonization by epiphytic lichens on regenerating trees is initially higher in stands that regenerated naturally compared with stands with artificial regeneration (plantations). However, in regenerating stands that are about 10 years older, no significant difference is found, and stands that are artificially regenerated exhibit relatively similar epiphytic communities compared with naturally regenerated stands. Consequently, using artificial reforestation measures when advance regeneration is deficient can provide adequate conditions for lichen colonization in stands that have been recently clearcut. However, it is noteworthy that in our study area, relatively large patches of virgin forest that could serve as sources of propagules were relatively abundant in the surrounding forest matrix. Our study did not allow us to evaluate if species colonization would be dispersal-limited in a more fragmented landscape where the connectivity between residual stands is interrupted, and when source habitats are located far apart from one another (see Gu *et al.*, 2001; Johansson and Ehrlén, 2003; Öckinger *et al.*, 2004). Similarly, colonization rates could be lower in a forest landscape dominated by relatively young forests which generally contain lower epiphytic lichen biomass (Boudreault *et al.*, 2009).

In order to insure recolonization of recently clearcut areas, we recommend, as a precautionary approach, to minimize the distance between regenerating stands and stands that constitute propagule sources, and to insure that there is a minimal proportion of mature and old stands that are maintained permanently at the landscape scale. Also, in a context where many uncertainties persist as to the size and spatial distribution of the remnant stands that will be left by forest harvestings in the future, it might be advisable to keep some veteran trees within recently cut stands, which might provide a local source of propagules for the inoculation of epiphytic lichens into regenerating forests (Hilmo and Såstad, 2001; Peck and McCune, 1997; Sillett and Goslin, 1999; Sillett *et al.*, 2000).

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3.9 Tables

Table 3.1 ANOVA summaries for the effects of regeneration type after harvesting (naturally regenerated stands and plantation) and time since harvesting (young and old) on stand, tree, and branch characteristics (n = 133 plots)

	dfn	dfd	F	p
Number of regenerating trees				
Regeneration type (R)	1	29	0.92	0.346
Time since harvesting (T)	1	29	8.55	**0.007**
R X T	1	29	0.56	0.462
Site (R X T)	29	96	26.62	**<0.001**
Diameter at breast height of regenerating trees				
Regeneration type (R)	1	30	4.29	**0.047**
Time since harvesting (T)	1	30	48.00	**<0.001**
R X T	1	30	15.29	**0.001**
Site (R X T)	30	96	7.49	**<0.001**
Tree height of regenerating trees				
Regeneration type (R)	1	30	1.91	0.178
Time since harvesting (T)	1	30	43.44	**<0.001**
R X T	1	30	11.62	**0.002**
Site (R X T)	30	96	6.21	**<0.001**
Branch age				
Regeneration type (R)	1	30	37.80	**<0.001**
Time since harvesting (T)	1	30	2.42	0.130
R X T	1	30	19.45	**<0.001**
Site (R X T)	30	99	8.01	**<0.001**
Branch diameter				
Regeneration type (R)	1	27	24.76	**<0.001**
Time since harvesting (T)	1	27	0.33	0.568
R X T	1	27	3.31	0.080
Site (R X T)	27	84	7.47	**<0.001**

Note: Significant effects ($p \leq 0.05$) are shown in boldface. The sampling site nested within the interaction of regeneration type and time since harvesting is a random factor. The random effects were used as error term when testing for differences between fixed effects. Dfn refers to degrees of freedom numerator and dfd refers to degrees of freedom denominator.

Table 3.2 Characteristics of the sampled stands and trees in naturally regenerated stands and in plantation in function of the time since harvesting (young and old)

	Naturally regenerated stands			Plantations			Differences between main factors
	n	Mean	SE	*n*	Mean	SE	
Number of regenerating trees (no./ha)							
Young	44	1440.9a	104.9	31	2185.5a	299.9	y < o
Old	28	3025.0a	393.2	26	3065.4a	415.0	n = p
Diameter at breast height (cm)							
Young	43	1.6b	0.1	31	0.93c	0.1	y < o
Old	30	2.4ab	0.2	26	2.90a	0.2	n > p
Tree height (cm)							
Young	43	188.7bc	4.6	31	161.8c	7.4	y < o
Old	30	234.7ab	8.2	26	293.6a	16.5	n = p
Branch age (year)							
Young	44	13.3a	0.6	31	5.1c	0.1	y = o
Old	32	10.7ab	0.7	26	8.7b	0.3	n > p
Branch diameter (cm)							
Young	39	0.88a	0.02	31	0.63a	0.01	y = o
Old	23	0.85a	0.03	26	0.71a	0.02	n > p

Note: ANOVAs were used to compare means between different age classes. The last column showed significant differences for the main factors (y = recent, o = old; n = naturally regenerated, p = plantation). Differences that were significant ($p \leq 0.05$) for the interaction between classes of regeneration type and time since harvesting according to least squares means Tukey's honestly significant difference tests are indicated by different letters for each variable.

Table 3.3 ANOVAs summaries for the effects of regeneration type after cutting (naturally regenerated stands and plantation), time since harvesting (young and old), and distance from the edge (5, 25, 50, and 100 m) on the number of thalli for each species and for foliose and fruticose lichen groups (n = 2569 branches)

	No. of thalli				No. of thalli		
	dfn	*F*	*p*		dfn	*F*	*p*
***Bryoria* spp.**				***Evernia mesomorpha***			
Regeneration type (R)	1	1.78	0.193	Regeneration type (R)	1	0.01	0.933
Time since harvesting (T)	1	2.15	0.153	Time since harvesting (T)	1	2.55	0.121
Distance (D)	3	3.34	**0.023**	Distance (D)	3	1.22	0.309
D X T	3	1.11	0.348	D X T	3	1.07	0.365
R X T	1	14.36	**0.001**	R X T	1	8.25	**0.007**
R X D	3	2.02	0.117	R X D	3	0.10	0.958
R X D X T	3	1.18	0.323	R X D X T	3	0.36	0.780
Site (R X T)	30	5.74	**<0.001**	Site (R X T)	30	4.76	**<0.001**
Site X D (R X T)	87	2.81	**<0.001**	Site X D (R X T)	87	1.85	**<0.001**
***Usnea* spp.**				**Fruticose lichens**			
Regeneration type (R)	1	2.50	0.125	Regeneration type (R)	1	5.24	**0.029**
Time since harvesting (T)	1	0.92	0.344	Time since harvesting (T)	1	0.53	0.470
Distance (D)	3	0.51	0.677	Distance (D)	3	0.69	0.558
D X T	3	0.56	0.643	D X T	3	1.31	0.275
R X T	1	11.17	**0.002**	R X T	1	9.98	**0.004**
R X D	3	0.84	0.478	R X D	3	1.13	0.343
R X D X T	3	0.48	0.699	R X D X T	3	1.28	0.285
Site (R X T)	30	3.55	**<0.001**	Site (R X T)	30	4.61	**<0.001**
Site X D (R X T)	87	2.20	**<0.001**	Site X D (R X T)	87	3.64	**<0.001**
Hypogymnia physodes				***Imshaugia aleurites***			
Regeneration type (R)	1	0.04	0.837	Regeneration type (R)	1	19.13	**<0.001**
Time since harvesting (T)	1	24.43	**<0.001**	Time since harvesting (T)	1	4.77	**0.037**
Distance (D)	3	0.26	0.855	Distance (D)	3	1.36	0.261
D X T	3	1.22	0.308	D X T	3	1.46	0.232
R X T	1	38.20	**<0.001**	R X T	1	7.32	**0.011**
R X D	3	1.10	0.355	R X D	3	1.25	0.297
R X D X T	3	0.34	0.794	R X D X T	3	1.57	0.202
Site (R X T)	30	4.89	**<0.001**	Site (R X T)	30	4.70	**<0.001**
Site X D (R X T)	87	3.50	**<0.001**	Site X D (R X T)	87	4.52	**<0.001**

Table 3.3 (continued)

	No. of thalli				No. of thalli		
	dfn	*F*	*p*		dfn	*F*	*p*
Parmelia sulcata				***Parmeliospis ambigua***			
Regeneration type (R)	1	1.59	0.218	Regeneration type (R)	1	19.19	**<0.001**
Time since harvesting (T)	1	8.69	**0.006**	Time since harvesting (T)	1	0.65	0.428
Distance (D)	3	2.00	0.121	Distance (D)	3	1.14	0.337
D X T	3	0.21	0.889	D X T	3	2.36	0.077
R X T	1	18.01	**<0.001**	R X T	1	13.41	**0.001**
R X D	3	0.02	0.995	R X D	3	0.11	0.953
R X D X T	3	0.82	0.485	R X D X T	3	1.92	0.133
Site (R X T)	30	1.71	0.029	Site (R X T)	30	7.99	**<0.001**
Site X D (R X T)	87	1.58	0.001	Site X D (R X T)	87	4.41	**<0.001**
Parmeliospis hyperopta				***Tuckermannopsis americana***			
Regeneration type (R)	1	18.69	**<0.001**	Regeneration type (R)	1	0.18	0.671
Time since harvesting (T)	1	0.61	0.440	Time since harvesting (T)	1	10.95	**0.002**
Distance (D)	3	0.33	0.805	Distance (D)	3	1.59	0.198
D X T	3	2.32	0.081	D X T	3	2.61	0.057
R X T	1	10.20	**0.003**	R X T	1	14.09	**<0.001**
R X D	3	0.23	0.878	R X D	3	0.70	0.555
R X D X T	3	1.25	0.296	R X D X T	3	0.11	0.955
Site (R X T)	30	7.75	**<0.001**	Site (R X T)	30	9.47	**<0.001**
Site X D (R X T)	87	2.61	**<0.001**	Site X D (R X T)	87	2.96	**<0.001**
Vulpicida pinastri				**Foliose lichens**			
Regeneration type (R)	1	22.51	**<0.001**	Regeneration type (R)	1	11.58	**0.002**
Time since harvesting (T)	1	0.17	0.685	Time since harvesting (T)	1	7.97	**0.008**
Distance (D)	3	0.38	0.765	Distance (D)	3	0.11	0.952
D X T	3	3.35	**0.023**	D X T	3	2.43	0.071
R X T	1	12.72	**0.001**	R X T	1	35.47	**<0.001**
R X D	3	0.58	0.629	R X D	3	1.21	0.311
R X D X T	3	2.19	0.095	R X D X T	3	1.44	0.237
Site (R X T)	30	6.95	**<0.001**	Site (R X T)	30	7.79	**<0.001**
Site X D (R X T)	87	3.64	**<0.001**	Site X D (R X T)	87	4.95	**<0.001**

Note: Significant effects ($p \leq 0.05$) are shown in boldface. Sampling site nested within the interaction of regeneration type and time since harvesting and the interaction of sampling site with distance nested within the interaction of regeneration type after cutting and time since harvesting were considered as random factors. The random effects were used as error term when testing for differences between fixed effects.

3.10 Figures

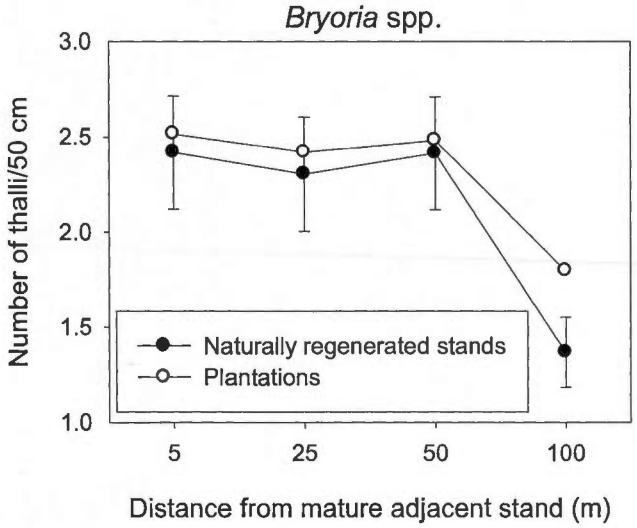


Figure 3.1 Changes of number of thalli in regenerating stands with increasing distance from adjacent mature stands. Data represent mean number of thalli and SE by distance (n = 2569 branches).

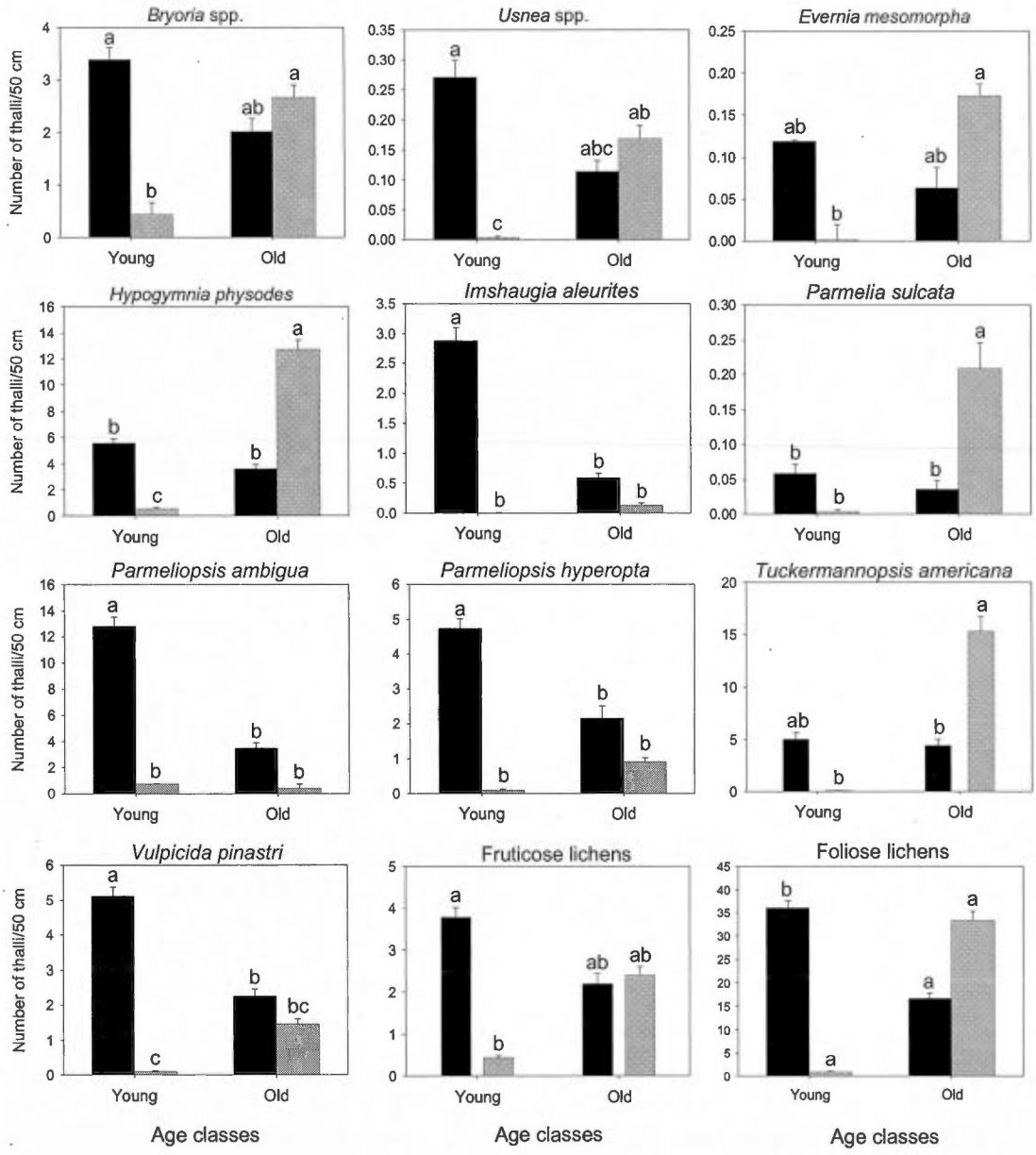


Figure 3.2 Mean number of thalli and SE by regeneration age class and by regeneration type for each lichen species, and for the foliose and fruticose lichen groups (n = 2569 branches). ANOVA models were used to compare means. Black bars represent number of thalli on naturally regenerated trees, and grey bars represent number of thalli on planted trees. Differences that were significant ($p \leq 0.05$) according to least squares means Tukey's honestly significant difference tests are indicated by different letters.

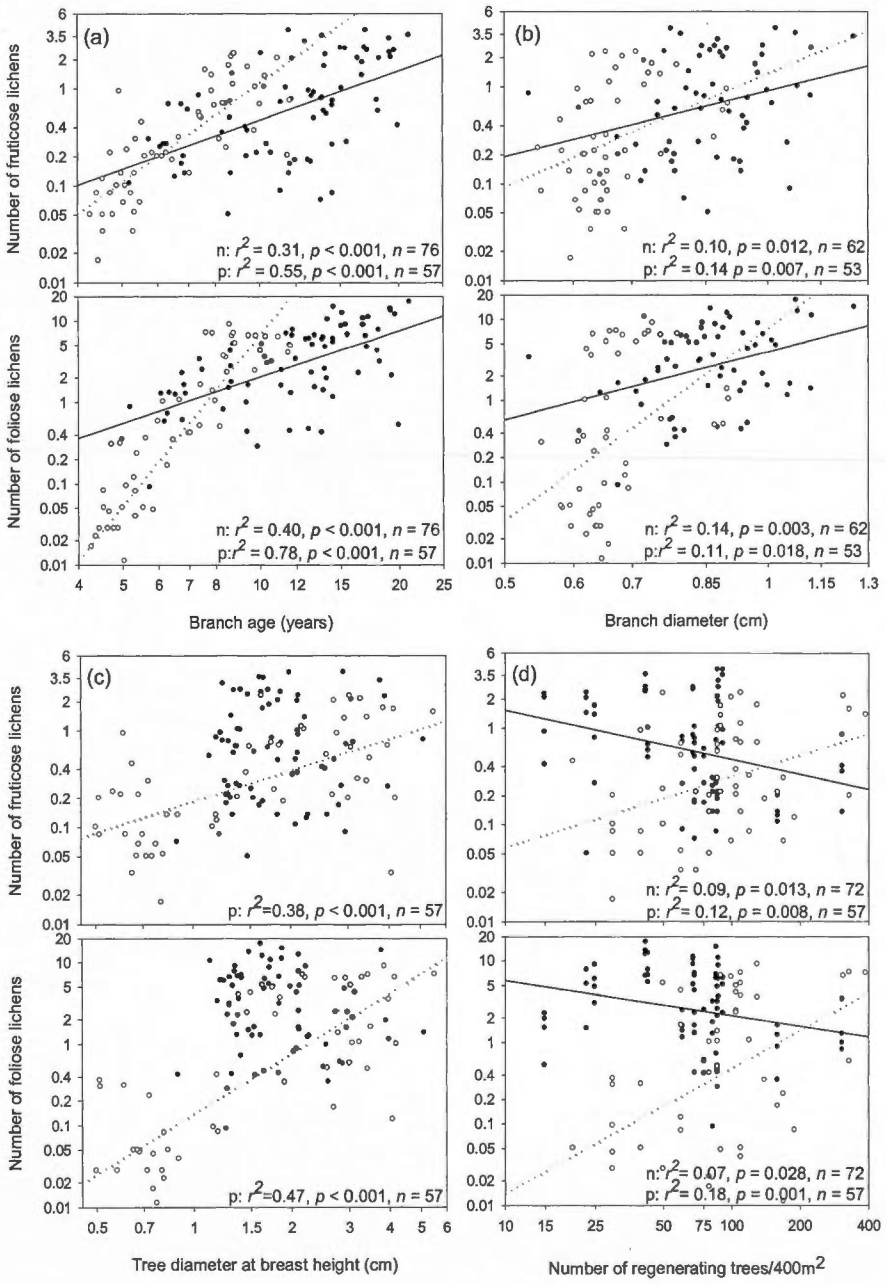


Figure 3.3 Linear regressions ($\log_{10}$ scale) of the number of lichen thalli against branch age (a), branch diameter (b), mean regeneration diameter at breast height (c), and number of regenerating trees (d) for the two regeneration types (natural regeneration: filled circles, a black regression line and an equation preceded by the letter 'n'; plantations: empty circles, dotted regression line and an equation preceded by the letter 'p'). Regression lines are only shown for significant relationships ($p \leq 0.05$).

3.11 Appendices

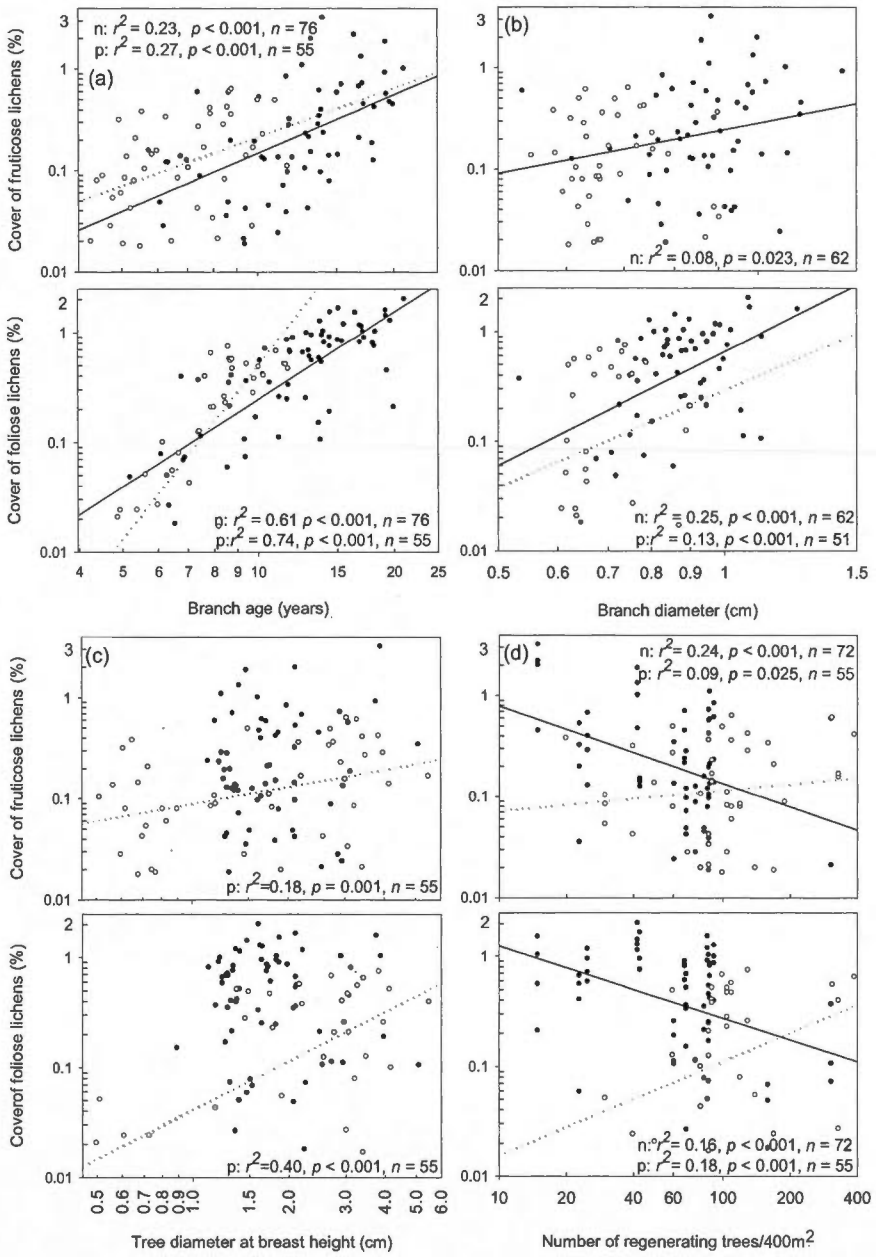
Appendix 3.1 ANOVAs summaries for the effects of regeneration type after cutting (naturally regenerated stands and plantation), time since harvesting (young and old), and distance from the edge (5, 25, 50, and 100 m) on cover of each species and for foliose and fruticose lichen groups (n = 2569 branches)

	Cover (%)				Cover (%)		
	df	*F*	*p*		df	*F*	*p*
***Bryoria* spp.**				***Evernia mesomorpha***			
Regeneration type (R)	1	2.08	0.160	Regeneration type (R)	1	0.02	0.899
Time since harvesting (T)	1	0.13	0.720	Time since harvesting (T)	1	2.33	0.137
Distance (D)	3	6.00	**0.001**	Distance (D)	3	1.46	0.233
D X T	3	0.40	0.756	D X T	3	0.99	0.404
R X T	1	7.31	**0.011**	R X T	1	6.55	**0.016**
R X D	3	0.97	0.410	R X D	3	0.03	0.992
R X D X T	3	0.63	0.598	R X D X T	3	0.26	0.857
Site (R X T)	30	5.72	**<0.001**	Site (R X T)	30	4.41	**<0.001**
Site X D (R X T)	85	2.41	**<0.001**	Site X D (R X T)	85	2.13	**<0.001**
***Usnea* spp.**				**Fruticose lichens**			
Regeneration type (R)	1	2.33	0.137	Regeneration type (R)	1	2.32	0.138
Time since harvesting (T)	1	0.98	0.331	Time since harvesting (T)	1	0.44	0.514
Distance (D)	3	0.57	0.633	Distance (D)	3	4.01	**0.010**
D X T	3	0.34	0.796	D X T	3	0.42	0.742
R X T	1	10.81	**0.003**	R X T	1	9.70	**0.004**
R X D	3	0.56	0.642	R X D	3	0.72	0.541
R X D X T	3	0.26	0.857	R X D X T	3	0.62	0.606
Site (R X T)	30	3.27	**<0.001**	Site (R X T)	30	5.19	**<0.001**
Site X D (R X T)	85	2.43	**<0.001**	Site X D (R X T)	85	2.72	**<0.001**
Hypogymnia physodes				***Imshaugia aleurites***			
Regeneration type (R)	1	3.93	0.057	Regeneration type (R)	1	22.52	**<0.001**
Time since harvesting (T)	1	18.73	**<0.001**	Time since harvesting (T)	1	4.53	**0.042**
Distance (D)	3	0.24	0.867	Distance (D)	3	0.98	0.407
D X T	3	0.71	0.551	D X T	3	0.72	0.541
R X T	1	38.70	**<0.001**	R X T	1	6.62	**0.015**
R X D	3	2.07	0.111	R X D	3	1.07	0.368
R X D X T	3	0.45	0.715	R X D X T	3	0.68	0.567
Site (R X T)	30	2.79	**<0.001**	Site (R X T)	30	3.60	**<0.001**
Site X D (R X T)	85	2.51	**<0.001**	Site X D (R X T)	85	3.83	**<0.001**

Appendix 3.1 (continued)

	Cover (%)				Cover (%)		
	df	*F*	*p*		df	*F*	*p*
Parmelia sulcata				***Parmeliospis ambigua***			
Regeneration type (R)	1	1.17	0.289	Regeneration type (R)	1	23.27	**<0.001**
Time since harvesting (T)	1	6.80	**0.014**	Time since harvesting (T)	1	0.88	0.357
Distance (D)	3	1.35	0.262	Distance (D)	3	2.04	0.114
D X T	3	0.20	0.895	D X T	3	2.00	0.120
R X T	1	17.11	**<0.001**	R X T	1	12.07	**0.002**
R X D	3	0.40	0.755	R X D	3	0.25	0.859
R X D X T	3	1.21	0.310	R X D X T	3	1.09	0.360
Site (R X T)	30	2.07	**0.005**	Site (R X T)	30	7.93	**<0.001**
Site X D (R X T)	85	1.27	0.054	Site X D (R X T)	85	2.83	**<0.001**
Parmeliospis hyperopta				***Tuckermannopsis americana***			
Regeneration type (R)	1	23.27	**<0.001**	Regeneration type (R)	1	0.02	0.891
Time since harvesting (T)	1	0.88	0.357	Time since harvesting (T)	1	10.47	**0.003**
Distance (D)	3	2.04	0.114	Distance (D)	3	0.97	0.413
D X T	3	2.00	0.120	D X T	3	1.42	0.243
R X T	1	12.07	**0.002**	R X T	1	13.46	**<0.001**
R X D	3	0.25	0.859	R X D	3	0.19	0.902
R X D X T	3	1.09	0.360	R X D X T	3	0.10	0.962
Site (R X T)	30	8.34	**<0.001**	Site (R X T)	30	5.53	**<0.001**
Site X D (R X T)	85	1.70	**<0.001**	Site X D (R X T)	85	3.15	**<0.001**
Vulpicida pinastri				**Foliose lichens**			
Regeneration type (R)	1	22.23	**<0.001**	Regeneration type (R)	1	23.22	**<0.001**
Time since harvesting (T)	1	0.08	0.776	Time since harvesting (T)	1	2.67	0.113
Distance (D)	3	1.59	0.198	Distance (D)	3	0.49	0.693
D X T	3	6.72	**<0.001**	D X T	3	2.16	0.099
R X T	1	11.92	**0.002**	R X T	1	28.44	**<0.001**
R X D	3	0.51	0.676	R X D	3	0.89	0.451
R X D X T	3	2.51	0.064	R X D X T	3	0.85	0.469
Site (R X T)	30	9.36	**<0.001**	Site (R X T)	30	7.19	**<0.001**
Site X D (R X T)	85	1.83	**<0.001**	Site X D (R X T)	85	4.09	**<0.001**

Note: Significant effects ($p \leq 0.05$) are shown in boldface. Sampling site nested within the interaction of regeneration type and time since harvesting and the interaction of sampling site with distance nested within the interaction of regeneration type after cutting and time since harvesting were considered as random factors. The random effects were used as error term when testing for differences between fixed effects.



Appendix 3.2 Linear regressions ($\log_{10}$ scale) of the lichen cover against branch age (a), branch diameter (b), mean regeneration diameter at breast height (c), and number of regenerating trees (d) for the two regeneration types (natural regeneration: filled circles, a black regression line and an equation preceded by the letter 'n'; plantations: empty circles, dotted regression line and an equation preceded by the letter 'p'). Regression lines are only shown for significant relationships ($p \leq 0.05$).

CHAPITRE IV

DO CANOPIES OPENED BY PARTIAL CUTTING PROVIDE GROWTH CONDITIONS SIMILAR TO OLD-GROWTH FORESTS FOR TWO EPIPHYTIC LICHENS IN BLACK SPRUCE BOREAL FORESTS?

Catherine Boudreault, Darwyn Coxson, Yves Bergeron, Suzan Stevenson et Mathieu Bouchard

En preparation pour soumission à Ecological Applications

4.1 Résumé

Nous avons examiné les taux de croissance de deux espèces de lichens épiphytes, *Bryoria nadvornikiana* et *Evernia mesomorpha*, en fonction de différents gradients d'ouverture du couvert dans des forêts boréales d'épinette noire de l'ouest du Québec. Les taux de croissance ont été évalués à partir de transplants installés dans deux types de peuplements, soit de vieux peuplements n'ayant jamais été coupés et des vieux peuplements récemment traités par coupe partielle. Les accroissements ont été mesurés sur une période de deux ans, et plusieurs variables environnementales (e.g. ouverture de la canopée, température des thalles, contenu en eau des thalles) ont été mesurées directement sur les sites. Les résultats indiquent que malgré une variation importante dans les taux de croissance chez les deux espèces de lichens dans les différents types de peuplements, la croissance des deux espèces était réduite dans les coupes partielles. La réponse négative est proportionnelle au degré d'ouverture dans le couvert dominant et *B. nadvornikiana*, une espèce généralement davantage associée aux couverts forestiers fermés, est significativement plus affectée qu'*E. mesomorpha*, une espèce plutôt associée aux couverts forestiers plus ouverts. Dans la discussion, nous soulignons que cette réponse négative contraste avec ce qui est généralement rapporté dans la littérature en ce qui concerne l'effet de la création d'ouvertures sur la croissance des lichens épiphytes. En fonction de l'analyse des différents paramètres environnementaux mesurés, nous suggérons que la réduction de la durée d'hydratation dans les coupes partielles, le risque accru de la fragmentation des thalles dans les coupes partielles, le climat relativement sec qui prévaut dans cette région, ainsi qu'une année particulièrement sèche lors de la deuxième année de l'étude peuvent expliquer ces résultats. Les résultats ne remettent pas en cause le fait que les coupes partielles peuvent contribuer au maintien des populations de lichens épiphytes au niveau du paysage, surtout lorsque l'on compare cette pratique aux coupes totales qui prévalent généralement dans cette région. Ils suggèrent néanmoins que, dans cette région, les peuplements récemment traités par coupe partielle offrent des conditions de croissance inférieures à celles que l'on retrouve dans les peuplements non coupés.

4.2 Abstract

We examined the growth rates of two epiphytic lichen species, *Bryoria nadvornikiana* and *Evernia mesomorpha*, as a function of different gradients of canopy opening in black spruce boreal forests of western Québec. Lichen growth rates were evaluated from transplants made in two stand types, old never-before harvested stands and old stands that were recently treated by partial cuts. The growth rates were measured over a period of two years and many environmental variables (e.g. canopy openness, thalli temperature, thalli wetness) were measured directly at the sampling sites. Despite differences in growth rates among transplants, we observed reduced growth rates in partial cuts for both species. This negative response is proportional to the degree of openness in the dominant canopy, and *B. nadvornikiana*, a species typically associated with relatively closed dominant canopies, was more affected than *E. mesomorpha*, a species that tends to be typically associated with open canopies. In the discussion, we emphasize that this negative response contrasts with what is generally reported in the literature about the effect of canopy opening creation on epiphytic lichen growth. As a function of the environmental parameters that were measured on site, we suggest that a reduction in duration of hydration period and increased risk of thalli fragmentation in partially cut stands, as well as relatively dry weather during the second year of the study, could explain this result. The results do not challenge the fact that partially cut stands can contribute in maintaining some lichen populations at the landscape level, especially when these cuts are compared with the clearcuts that are generally used in the region. This study nonetheless suggest that, in this region, stands recently treated with partial cuts offer growth conditions that are inferior to those usually found in uncut stands.

4.3 Introduction

Epiphytic lichen biomass accumulation in natural forests generally increases with stand age (Esseen *et al.*, 1996; Peterson and McCune, 2001; Moning *et al.*, 2009). Many lichen species have limited propagule dispersal capabilities, or can be highly dependent on structural attributes or microclimatic conditions present only in old-growth stands. At the landscape scale, populations of epiphytic lichens are thus potentially affected by the increasing rarity of old-growth stands (Dettki *et al.*, 2003). At the stand scale, within the remaining old-growth patches, small-scale disturbances such as partial cuts or natural mortality can also have an effect on epiphytic lichen populations by modifying local environmental conditions. Lichens are especially sensitive to small changes in gradients of light, temperature and moisture availability, which can have major impacts on lichen growth (Coxson and Stevenson, 2007a). Understanding the impact of small-scale disturbances on epiphytic lichen growth may have important management implications in selecting the type of forestry interventions that are compatible with the maintenance of residual populations of epiphytic lichens.

Epiphytic lichens are poikilohydric organisms, meaning that they are unable to regulate their uptake or loss of moisture, and depend on atmospheric sources for water and inorganic nutrients (Nash, 2008). Hydration can result from direct precipitation interception, from dewfall formation on thallus surfaces, from melt of snowfall or ice, and from direct uptake (for thalli with green algal photobionts) of water during periods of high atmospheric humidity (Nash, 1996; Kershaw, 1985). Lichens generally spend short periods of time being photosynthetically active, i.e. when they are both wet and illuminated (Farrar, 1976), and a major limitation of lichen growth is the time period during which the lichen is metabolically active (Palmqvist and Sundberg, 2000). Achieving positive net assimilation of carbon during periods of thallus hydration depends upon the balance between photosynthesis and respiration. For instance, Lechowicz (1981) observed a net loss of thallus biomass in the arctic lichen *Cetraria cucullata* after thalli faced prolonged periods of respiratory carbon loss

without sufficiently long periods favourable for net photosynthesis activity. Long lasting rain or excess water may also adversely affect epiphytic lichens (Farrar and Smith, 1976; Goward, 1998; Gauslaa 2002). For instance, Goward (1998) speculated that dieback episodes in canopy *Bryoria* are the result of exposure to prolonged wet conditions.

Factors other than hydration can have an influence on lichen growth. Low light conditions are known to restrict growth of species of epiphytic lichens in coniferous forests (Gaio-Oliveira *et al.*, 2004; Gauslaa *et al.*, 2006; Gauslaa *et al.*, 2007; Jansson *et al.*, 2009). For example, Coxson and Stevenson (2007) found that *Lobaria pulmonaria* growth in old-growth cedar–hemlock forests increases with greater canopy light transmission; high light environments can result in sustained high growth rates in open habitats for species associated with old forests (e.g., *Lobaria pulmonaria* [Gauslaa *et al.*, 2006], *Usnea longissima* [Keon and Muir, 2002]) even if these species rarely occur within these habitats. However, exposure to high irradiance can enhance the evaporative losses of water (Palmqvist, 2000) and more rapid drying of lichen thalli can have a negative impact on lichen growth (Coxson *et al.*, 2003). Temperature appears to be less important than water and light for lichen growth (Nash, 1996). However, the increase in temperature above the thermal optima of the lichen can also increase the respiration rate and diminish the net photosynthesis (Nash, 1996). Biomass accumulation for canopy lichens can also be constrained by thallus fragmentation. Thallus fragmentation by wind, water, or ice is particularly important for thin and finely dissected lichens such as *Alectoria sarmentosa* and many *Bryoria* species (Esseen, 1985).

In the eastern part of the Canadian boreal forest, the proportion of mature and old forest habitat is declining due to the combined influence of severe disturbances such as fire and clear cutting (Bergeron *et al.*, 2002; Cyr *et al.*, 2009). This decline has potentially serious consequences for canopy lichen communities (Dettki *et al.*, 2003), and the question of whether the remaining habitats are still suitable for lichen populations becomes more acute. Partial disturbances occurring in the remaining mature to old-growth stands, either from a natural or an anthropogenic origin, could affect epiphytic lichens in different ways. Because

of their potential for increase in growth with greater canopy openness, some authors found that partial cutting might create much better conditions for epiphytic lichens than clear cutting (Coxson *et al.*, 2003; Stevenson and Coxson, 2003; Rominger *et al.*, 1994; Coxson and Stevenson, 2005; Stevenson and Coxson, 2007; Muir *et al.*, 2006; Stone *et al.*, 2008). However, in some circumstances, the abrupt creation of canopy openings could negatively impact the growth or the vitality of canopy lichens (Hedenås and Ericson, 2003, Coxson and Stevenson 2005, Lõhmus *et al.*, 2006), and could thus potentially affect population dynamics within the remaining patches of mature forests. It is necessary to verify the effect of partial canopy disturbances of various intensities on epiphytic lichen species associated with mature to old boreal forests of eastern Canada, where very few studies of this type have been undertaken so far.

We implemented a partial cutting experimental with diverse removal intensities to study the response of epiphytic lichens to changes in canopy openness in the Abitibi region of northern Quebec (Fenton *et al.*, 2009). The general objective of this study was to evaluate the response of two epiphytic lichens with different ecological requirements, *Bryoria nadvornikiana* (Gyelnik) Brodo & D. Hawksw. and *Evernia mesomorpha* Nyl., to canopy openness. We address two major hypotheses in this study: (1) that the growth of *B. nadvornikiana*, a species typically associated with closed-canopy forests, will be lower in the opened forest canopies than the growth of *Evernia mesomorpha*, a species more commonly associated with open-canopy forests, and (2) that the growth of the two species will be favoured when small increases in canopy openness occur, but will decline above some threshold. Results showing comparable growth between partial cuts and control forests would indicate that partial cuttings may maintain an adequate environment for epiphytic lichen growth and are a good alternative to generalized use of clear cutting to maintain the environment associated with old forests.

4.4 Methods

4.4.1 Study area

The study was conducted in the western part of the bioclimatic region of *Picea mariana*-feather moss forest in Quebec (50°00"N, 76°00"–80°00"W) (Saucier and Robitaille, 1998). The study area is also part of the northern Clay Belt (Rowe, 1972), a broad physiographic unit characterized by lacustrine deposits from proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). Clay soils predominate, the topography is relatively flat, and the forest mosaic is dominated by black spruce (*P. mariana*) stands. Jack pine (*Pinus banksiana*) stands dominate drier sites such as outwash deposits, old beaches, and eskers (Rowe, 1972). Meteorological stations located at La Sarre and Matagami, close to our study sites (Figure 1), indicate mean annual temperature (1971-2000) of 0.7 and -0.7 °C respectively, and mean total annual precipitation (1971-2000) of 890 and 906 mm, respectively (Environment Canada, 2004).

We studied lichen growth at three sites which are located more than 50 km from one another (Figure 4.1). Two of these sites were located in the western part of the Abitibi region (Muskuchii and Fénélon), north of the municipality of La Sarre. The other site was located in its eastern part, near the municipality of Lebel-sur-Quévillon (Maïcasagi). Each site contains a block of at least 25 ha of stands treated with partial harvests, and a block of at least 25 hectares where no harvest was done, and which was used as a control. The Muskuchii site was harvested with a diameter limit cut in which stems > 9 cm in diameter were harvested. This type of cutting left a residual stand that was heterogeneous, with sectors with very high retention and others with none (Fenton *et al.*, 2009). "Adapted cuts" were used at Fénélon and Maïcasagi. In this system, a certain proportion of stems in all diameter class are retained, resulting in a more even cover and in the retention of larger stems (Fenton *et al.*, 2009). The proportion of basal area removed in the partial cuts was 45% at Maïcasagi, 66% at Muskuchii, and 85% at Fénélon. The selected sites provide a gradient of canopy removal (and therefore openness) sufficient to test our hypotheses.

These sites were part of a larger study on the effects of tree removal on stand dynamics (windthrow, tree vitality, etc.), and the plot selection procedure is detailed in Fenton *et al.*, (2009). Within each of the three sites, we conducted lichen growth studies in 12 circular 400 m^2 plots located in partially cut treatments, and 12 plots located in uncut control treatments, for a total of 72 plots. All plots were dominated by black spruce. Each sample plot was located at least 100 m from the main roads to avoid any edge effect. Stand density and basal area after removal were measured inside each plot.

4.4.2 Lichen sampling

Growth rates (GR) of *Evernia mesomorpha* and *Bryoria nadvornikiana* were assessed with repeated measurements of transplants attached to artificial substrates. These two fruticose species were selected because their ecological requirements are different and we expected that their responses to canopy openness would also differ. The former has yellowish green color and a relatively robust and pendant or shrubby thallus, while the latter is pale grey, and has a finely dissected shrubby to almost pendant thallus (Brodo *et al.*, 2001). *E. mesomorpha* is a species associated with open canopy forests whereas *B. nadvornikiana* is more often found in closed and humid forests (Brodo *et al.*, 2001). We collected thalli of *E. mesomorpha* and *B. nadvornikiana* in undisturbed forests at the three sites in order to minimize the effects of transplantation. Thalli approximately 3 cm long were collected between 1.5 and 3 m above ground. Under a dissecting microscope, collected thalli were cleaned of bark fragments, needles, and other debris. Samples were weighted to the nearest 0.0001g after being placed in a growth chamber (relative humidity maintained at 60%) for 48h. We glued the lichens to glass tubes 3.6 cm long and 1.6 cm (outside dimension) in diameter with fungicide-free silicone. We then placed the lichen-tube assemblies in the growth chamber for 1 week to allow the mass to stabilize (Stevenson and Coxson, 2003). After one week, the assemblies were reweighed and placed in cages covered with 4-mm polypropylene landing net mesh in order to protect them from physical injuries. Glass tubes fit into snaps at the top of the cages. For more details on this method see Stevenson and Coxson (2003).

We placed two or three lichen-tube assemblies of each species in each plot. Transplants were installed at the same site where they had been collected. We randomly selected two or three trees in each plot in which to install lichens transplants. A wooden plank (2 m x 5 cm x 1 cm) was fixed horizontally on the trunk of each tree at a height between two and three meters. A lichen cage was attached to each end of each plank with a nylon cord. Lichens were first placed in their cages in mid-July 2004. The lichens were brought to the laboratory in fall 2004, held in the growth chamber at a relative humidity of 60% for at least 48h, reweighed, and returned to the exact location in the field. The same procedure was conducted for other seasons (summer 2004: from mid-July 2004 to the end of October 2004; winter 2004: from November 2004 to mid-May 2005; summer 2005: from mid-May 2005 to September 2005; winter 2005: from September 2005 to May 2006). The experiment ended in May 2006, when the samples were brought back in the laboratory for viability analysis.

The expression lichen growth rate used in this study incorporates mass changes resulting from two different processes: 1) gains from net photosynthesis and losses from dark and photorespiration and 2) losses in mass resulting from thallus fragmentation. For simplicity, we used the term 'growth' to indicate both increases and losses of biomass.

4.4.3 Canopy microclimate

Canopy microclimate measurements were taken from September 2004 to May 2006 in four plots: two at the Muskuchii site and two at the Maïcasagi site. At each site one representative control plot and one representative partial cut plot were chosen to measure canopy microclimate. To measure lichen temperature, hydration of lichen thalli, and light intensity, instrumentation was installed on two trees per plot on branches located between 2 and 4 m high. The instrumentation was distributed over all aspects. Lichen temperature was measured using fine-wire thermocouples (Omega Engineering, Stanford, CT) held against lichen thallus surfaces (2 to 3 lichens of each species per tree). The water content (WC) of lichen thalli was measured using an impedance technique (Coxson, 1991), adapted for alectorioid lichens (Campbell and Coxson, 2001), in which small clips provide measurements of electrical

conductivity across lichen thalli (2 to 3 lichens of each species per tree). PAR LITE sensors (Campbell Scientific) were used for measurements of photosynthetically active radiation (PAR). Two PAR LITE sensors were installed on the upper surface of a branch, at 3 m above ground, of the two selected trees. Air temperature and relative humidity were also measured at each site with a Campbell Scientific HMP45CF probe located on a tower in the middle of the plot at 3.5 m above ground. Instrumentation signals were recorded using Campbell Scientific CR-7 and CR-10x dataloggers.

At each cage location, a hemispherical (fisheye) photograph was taken to measure the percentage of canopy openness. The camera was fixed on a pole and levelled in all directions before taking the pictures. Photographs were taken during a two-week period during summer 2006 when the sky was cloudy. Photographs were analysed with Gap Light Analyzer 2.0 (http://www.rem.sfu.ca/forestry/index.htm).

4.4.4 Viability analysis

B. nadvornikiana and *E. mesomorpha* thalli were assessed for viability at the time of their final collection from the field by measuring net photosynthesis and dark respiration under homogeneous experimental conditions. By measuring net photosynthesis and dark respiration under homogeneous experimental conditions, we evaluated if transplants experienced conditions that stressed one or both bionts. If transplants are physiologically stressed they will show lower rate of photosynthesis or higher rate of dark respiration (D. Coxson, personal communication).

Net photosynthesis was assessed at 12°C and 200 umols $m^{-2}s^{-1}$ PAR, and dark respiration was assessed at 12°C and 0 umols $m^{-2}s^{-1}$ PAR. Temperature and light levels for the incubations are representative of cool overcast (non-stressful) summer conditions. Gas exchange was measured in closed-cell incubation chambers (Larson and Kershaw, 1975). Thalli were held at optimal levels of hydration, to avoid diffusive resistance to CO_2 uptake commonly observed in saturated thalli.

4.4.5 Statistical analyses

Forest characteristics and microclimate – Differences in stem density, basal area, and canopy openness between treatments were tested with two-wayANOVAs with treatment (partial cut plots and control plots) as main effect, and site (Muskuchii, Fenelon, and Maïcasagi) and sampling plot nested within the site as random effects.

Because our instrumentation was only installed in autumn 2004, we used climatic data collected at Matagami weather station (Environment Canada, 2010) to compare precipitations and temperatures in 2004 and 2005. For measurements performed on lichen samples, we report results for three different periods (October 2004, April 2005, and July 2005) when all sensors and dataloggers from partial cuts and control plots at Maïcasagi were working. Replicate measurements of lichen thallus temperature and hydration for each species and PAR were pooled within each site. Comparative thallus water content and mean duration of thallus hydration are presented for the first month of measurement only (October 2004), insuring that all measurements derive from clip placements on viable thalli (thalli can degrade over time with extended clip placement). A threshold of 5% thallus hydration (i.e. water content in relation to dry weight) was used to separate records for "dry" lichens from those for "wet" or hydrated lichens. This threshold corresponds to the point below which little physiological activity (gas exchange) is detectable in these species (D.S. Coxson, personal observation).

Lichen growth – Repeated measure analyses were used to examine between-group differences (treatments) and within-group differences (season of measurement) in lichen biomass. Treatment and season were fixed factors, and site and sampling plot nested within the site were random factors. Number of days within each season was used as a covariable to account for differences in length of seasons. The response variable was expressed as the biomass of each transplant at the end of each season minus its initial biomass at the beginning of the experiment. Lichen assemblies that were damaged by events such as tree-fall or cage-fall were excluded from the data set. Transplants that showed anomalously low growth rates

were considered outliers (biomass >2 SD below the mean biomass of all transplants in each season [Stevenson and Coxson, 2003; Muir *et al.*, 2006]) and were also removed from the data set. Data were square root transformed to satisfy the assumptions of ANOVA for all repeated measured analyses.

Growth rates (GR) of both species at the end of the experiment were tested with a nested mixed ANOVA with treatment as fixed effect and site as random effect. Response variables for this analysis were the total growth rate per cage for each species. Growth rate was calculated as

$$GR = (W2 - W1)/W1 \times 100$$

where $W1$ is lichen weight at the beginning of the experiment and $W2$ is lichen weight at the end of the experiment. Data transformation was not necessary to satisfy the assumptions of normality of the distributions and homoscedasticity of the variance. Lichens with biomass >2 SD below the mean biomass of all transplants were removed from the data set. When we calculated annual or seasonal growth rates, we considered $W1$ to be lichen weight at the beginning of each year or season, and $W2$ lichen weight at the end of each year or season.

All ANOVA analyses were performed with the MIXED procedure of SAS (SAS Institute, 2002). Denominator degrees of freedom were calculated using Satterthwaite's approximation (Littell *et al.*, 1996). The random effects were used as error term when testing for differences between fixed effects. Significant differences ($p \leq 0.05$) within fixed effects were detected with ls means Tukey HSD tests.

Chi-square tests were used to compare frequencies of negative growth rate (or zero growth rate) between treatments (partial cuts and control plots for the three sites combined) (1) for each season, (2) at the end of each year, and (3) at the end of the experiment. Lichens with biomass >2 SD below the mean biomass of all transplants in each season were included in

this analysis. Pearson chi-square components (X^2: $[O - E]^2/E$) were used to measure the difference between observed (O) and expected (E) values.

Viability analysis – One-way ANOVA was used to test for differences between treatments in net photosynthesis and dark respiration for each species. Data transformation was not necessary to satisfy the assumptions of normality and homoscedasticity.

4.5 Results

4.5.1 Site structural characteristics

Canopy openness ($F_{1,50.8} = 83.16$, $p < 0.001$), stem density ($F_{1,20.6} = 69.98$ $p < 0.001$), and basal area ($F_{1,29.8} = 75.93$, $p < 0.001$) differed significantly across treatments. Tree density and basal area were respectively two and three times higher in control plots while canopy openness was two times higher in partial cut plots compared with control plots (Table 4.1). Canopy openness ($F_{2,42.1} = 15.78$, $p < 0.001$) and stem density ($F_{2,44.4} = 6.94$ $p = 0.002$) differed also across sites. Canopy openness was highest in Fénélon site and stem density in Muskuchii site (Table 4.1). Basal area did not differ much between sites, both in controls and partial cuts (Table 4.1).

4.5.2 Microclimatic conditions

The Matagami weather station recorded more precipitation and lower temperatures during summer 2004 than in summer 2005 (Fig. 4.2). June was particulary warm in 2005 with a mean temperature of 16.6°C compared to 11.4°C in 2004. Summer total precipitation (June, July and August) in 2004 was twice higher than in summer 2005.

In general, for October 2004, April 2005, and July 2005, lichen temperatures, air temperature, and PAR were higher in partial cuts than in control plots; conversely, air humidity was higher in control plots (Fig 4.3). The same pattern was observed for Muskuchii site (results not

shown). Water content of each species during October 2004 was generally higher in control plots at both sites (Fig. 4.4).

Duration of hydration during October 2004 was significantly higher in control plots than in partial cuts ($F = 6.54$, $p = 0.017$). During this month, lichens were hydrated 18.2% (SD = 5.5%) of the time in control plots compared with 14.5% (SD = 3.8%) in partial cuts. There was no significant difference between *B. nadvornikiana* and *E. mesomorpha* in terms of duration of hydration ($F = 0.16$, $p = 0.694$).

4.5.3 Growth of transplants

Repeated measures analyses showed that growth differed significantly across treatments for *B. nadvornikiana* (Table 4.2). Biomass was also significantly higher in control than in partial cut plots. Growth of *B. nadvornikiana* differed significantly across seasons (Table 4.2). Growth of the two species was higher in summer than during winter, and higher during the first summer compared with the second summer. The significant interaction between season and treatment indicates that the difference between treatments in *B. nadvornikiana* growth varied across seasons (Fig. 4.5): differences between treatments were significant during the second summer and second winter. Repeated measures analyses also showed that growth differed significantly across treatments for *E. mesomorpha* (Table 4.2) and the growth was higher in control plots than in partial cuts. Differences between treatments of *E. mesomorpha* growth varied also across seasons with significant differences during the second summer and second winter (Table 4.2).

Mean GR for *B. nadvornikiana* and *E. mesomorpha* during the first year were respectively 13.3% and 7.4% in control plots comparatively to 5.6% and 5.2% in partial cuts (Fig. 4.5). Mean GR during the second year for *B. nadvornikiana* and *E. mesomorpha* were respectively 5.7% and 7.3% and -8.3% and 0.8% in control plots and partial cuts (Fig. 4.5). Total growth after two years was more than 2.5 times higher in control plots (*B. nadvornikiana*: 18.6% and *E. mesomorpha*: 13.7%) than in partial cuts (*B. nadvornikiana*: -5.0% and *E. mesomorpha*:

5.4%; Fig. 4.5). However, growth responses after two years were highly variable in both treatments and for both species as shown by large SD in the two last columns of Figure 4.5. Maximal seasonal GR for individual thalli were 71.2% for *B. nadvornikiana* and 31.8% for *E. mesomorpha*,

ANOVA performed on total GR after two years showed significant differences between treatments (*B. nadvornikiana*: $F_{1,148} = 32.65$, $p < 0.001$; *E. mesomorpha*: $F_{1,122} = 10.41$, $p = 0.002$) with higher GR for *B. nadvornikiana* and *E. mesomorpha* in control plots compared with partial cut plots (Fig. 4.5). There was a significant difference among sites for *E. mesomorpha* ($F_{2,122} = 5.96$, $p = 0.003$) but not for *B. nadvornikiana* ($F_{2,147} = 1.12$, $p = 0.329$). Growth rate of *E. mesomorpha* was significantly lower in the Muskuchii site compared with the Fénélon and Maïcasagi sites.

Total GR of *B. nadvornikiana* and *E. mesomorpha* decreased significantly with canopy openness (Fig. 4.6a and 4.6b). Canopy openness over 40% and 70% resulted in negative GR for *B. nadvornikiana* and *E. mesomorpha*, respectively (Fig. 4.6). GR of *B. nadvornikiana* showed a positive relationship with basal area and stem density, while GR of *E. mesomorpha* showed no relationship with stem density, and a positive but weak relationship with basal area.

Figure 7 shows the proportion of thalli that experienced negative or null GR in the two treatments. There was a significantly higher number of *B. nadvornikiana* thalli ($p < 0.05$) with negative GR in partial cuts than in control plots for all seasons, at the end of the first and second years, and at the end of the experiment. Number of *E. mesomorpha* thalli with negative or zero GR values was significantly higher ($p < 0.05$) in partial cuts than in control plots for all seasons (except during the first summer where this trend was reversed), at the end of the second year, and at the end of the experiment; the analysis was not significant ($p = 0.732$) for the first year. Number of transplants that lost weight was higher during the second year in both treatments for *B. nadvornikiana* and *E. mesomorpha* (Fig. 4.7). At the end of the experiment, 63.2% of *B. nadvornikiana* and 44.0% of *E. mesomorpha* located in partial cut

plots lost weight vs. 23.8% for *B. nadvornikiana* and 16.9% for *E. mesomorpha* in control plots.

4.5.4 Lichen viability

There was no significant difference in net photosynthesis and in dark respiration between transplants coming from the different treatments for both species (Table 4.3), suggesting that when environmental conditions such as light, humidity and temperature are controlled for, the transplants exhibited a similar viability at the end of the experiment.

4.6 Discussion

In this study, we found a high variability in growth responses of the two lichens, both between treatments and sites. This is not surprising in the light of the large number of sample plots used, representing the variability in environmental conditions in old-growth and partially cut black spruce stands in this region. A major advantage of this study is that growth responses were followed during two years in the same transplants. By this it was possible to assess the influence of between-year variation in climates on treatment effects on lichen growth. In this discussion we will first summarize trends that emerged from the analyses and compare them with what was observed in other studies done in comparable regions, and then we will examine the environmental factors that may explain the observed growth responses.

4.6.1 Observed trends

Our results indicate that after two years, growth rates of both species were significantly higher in control plots than in partial cuts. The growth of both species decreases linearly with canopy openness. As expected, the species that is usually associated with closed canopy forests, *B. nadvornikiana*, was more affected by increases in canopy openness than was the species associated with open canopy forests, *E. mesomorpha*. Overall, the hypothesis that canopy openness could increase lichen growth was not validated for these species in our experiment.

The mean growth rates found in natural forests of this study (control plots), 7.3% for *E. mesomorpha* and varying between 5.7 and 13.3% for *B. nadvornikiana* depending on the years are comparable to those found in other studies of epiphytic lichens. Renhorn and Esseen (1995) evaluated the annual growth rate of five alectorioid boreal lichens, which varied between 6.3 and 16.3 %. These authors also found that mean growth of *Bryoria fuscescens* was 8.2%, while Stevenson and Coxson (2003) found a growth rate of 6.6% for the same species.

Variable responses of epiphytic lichen growth to canopy removal were reported in the literature. For instance, Rominger *et al.* (1994) found no significant changes in the biomass of *Alectoria* and *Bryoria* 8–10 years after partial cutting in subalpine spruce–fir forests of the Pacific Northwest, but they identified a shift in genus composition towards an increased proportion of *Bryoria* biomass. The same phenomenon was observed by Stone *et al.* (2008) four years after partial cutting in Québec's Gaspé Peninsula. In British Columbia, Coxson *et al.*, (2003) found that partial cutting with 30% removal within a subalpine spruce–fir forest did not have a significant effect on lichen loading in residual trees and on canopy microclimate. Stevenson and Coxson (2007) found that the increased exposure associated with partial cutting in British Columbia promotes the growth of *Bryoria* on the residual trees, at least for the first 30 years, with the greatest rate of accumulation in partial cuts with low level of green tree retention (< 10 m^2/ha) compared with the ones with higher residual basal areas (> 20 m^2/ha). In Sweden, a negative effect of partial cutting on vitality and radial growth of three out of five species was observed by Hedenås and Ericson (2003) on *Populus tremula*, and, in Norway, Gauslaa *et al.* (2006) found that the creation of small openings by partial cut harvesting may result in conditions favourable for *L. pulmonaria*.

4.6.2 Influence of environmental factors

Canopy removal influences epiphytic lichen development through changes in microclimatic conditions. Because lichens are poikilohydric organisms, lichen growth is particularly influenced by factors such as humidity, light and temperature levels. Microclimate during

periods of metabolic activity must be adequate to allow gains of carbon that are sufficient to balance the losses caused by respiration (Lechowicz, 1981) and thallus fragmentation (Gauslaa *et al.*, 1997). Changes in microclimate could also have an effect on thallus fragmentation. The main environmental factors that could affect lichen growth are addressed successively in the following sections.

Decrease of air humidity and water content with canopy openness – Water availability is crucial for lichen growth (Green and Lange, 1994; Palmqvist, 2000). The greater insolation exposure experienced by lichen transplants in partial cuts, combined with lower relative air humidity in these treatments, have probably contributed to faster desiccation in partial cuts compared with control plots. Creating openings in the dominant canopy may also have increased wind penetration, which could have reduced the duration of lichen hydration periods (Stevenson and Coxson, 2007). Water absorption and desiccation are rapid in finely dissected fruticose lichens with a high area to weight ratio, such as those used in this study (Palmqvist, 2000; Gauslaa *et al.*, 2006). In our study, we found that the duration of hydration of lichens in partial cuttings was shorter than in control plots. Because lichen growth is limited by the duration of hydration periods and by the irradiance level during these periods (Gauslaa *et al.*, 2007), a reduction of the hydration period diminishes the time available for photosynthetic activity and lichen growth (Lange *et al.*, 1986). Hydration periods of sufficient length also play an important role for the lichen to be able to repair damage due to excess light (Gauslaa *et al.*, 2006).

Lichen growth rates observed in this study changed across seasons, with the highest growth rates observed during the first summer. Other studies have shown that growth response is highly seasonal. For instance, *Lobaria pulmonaria* growth is rapid during moist seasons and slow during dry ones (Gauslaa *et al.*, 2006). During the first summer of our study, growth rates of both species were not significantly different between treatments. Growth of *E. mesomorpha* was even slightly higher in partial cuts. It is thus possible that greater light availability has, in the short-term, increased the growth of both species. For both species and

both treatments however, growth rate was much lower during the second summer. Summer 2005 was relatively warm and dry comparatively to summer 2004 (see Fig. 2). In fact summer 2005 (June, July, and August) was the dryest and the warmest of the last decade (2001-2010), with mean precipitation per month of 63.5 mm compared with 93.3 mm for the decade (Environment Canada, 2010). Consequently, the effect of desiccation in partial cut treatments and its subsequent influence on lichen growth may have been exacerbated during the second year of our experiment. This might partially explain why the negative trend in growth rate with canopy openness was generally more pronounced in our study compared with what was observed elsewhere.

Studies on vertical zonation in western Canada have shown that *Bryoria* species may be excluded from lower canopy positions due to intolerance to prolonged hydration periods (Goward, 1998; Campbell and Coxson, 2001; Coxson and Coyle, 2003) and they are more abundant in more exposed habitats such as mid and upper tree canopy positions. Other studies have shown that the increased exposure associated with partial cuttings in northern British Columbia has favored the growth of *Bryoria* on residual trees (Stevenson and Coxson, 2007). It is possible that partial cuts in our experiment may have promoted the growth of some *Bryoria* species, but because the species we studied (*Bryoria nadvornikiana)* is a shade tolerant species, largely absent from open sites, and abundant in humid southern boreal forests (Brodo and Hawksworth, 1977), it is likely that it is more tolerant of prolonged wetting and more sensitive to desiccation than many other *Bryoria* species.

The relatively dry climate and limited precipitation observed in this region (around 900 mm) may also have increased lichen vulnerability to micro-environmental modifications. Lichens may be able to withstand more open conditions in more humid climates. For instance, at Pinkerton Mountain in British Columbia, where the annual mean precipitation is around 1400 mm, Stevenson and Coxson (2003) found as high a growth rate of *Bryoria fuscescens* and *Alectoria sarmentosa* in the single-tree selection area as in the unlogged control area.

Increase of light with canopy openness - Once wet and metabolically active, lichen growth is limited primarily by light (Palmqvist, 2000). Because photosynthesis in lichens is often light limited (Gaio-Oliveira *et al.*, 2004; Gauslaa *et al.*, 2006), we expected an increase of lichen growth with canopy openness. However, in our study, it is possible that exposure to high irradiance enhanced the evaporative losses of water and offset net assimilation gains realized from greater light availability by limiting the duration of physiological activity. In this situation, photosynthesis could have been limited to periods with relatively low irradiances, such as during rainfall or during the early morning hours (Palmqvist, 2000).

Photoinhibition sensitivity is another factor that must be considered after a modification in canopy structure. In our study, viability results at the end of the experiment and under control conditions in laboratory indicate that lichens in partial cuts do not show any obvious stress response, such as elevated rate of respiration or reduced rate of photosynthesis. Lichens have different strategies to cope with increases in light levels: they can increase thallus thickness (Hyvärinen, 1992) and chlorophyll a/b ratio (Gauslaa *et al.*, 2006), or they can produce pigments which act as sunscreen for photobiont cells such as melanin and parietin (Solhaug and Gauslaa, 1996, Gauslaa and Solhaug, 2001; Hilmo, 2002; Coxson and Stevenson, 2007a). In general, lichens acclimated to open and sunny habitats experience prolonged high light exposure without serious or lasting level of photoinhibition (Gauslaa *et al.*, 2001) contrary to shade-adapted species (Gauslaa and Solhaug, 1999). Furthermore, a majority of brightly coloured usnic-acid containing lichens of sun-exposed habitats such as *E. mesomorpha* never turn brown, suggesting that usnic acid is an efficient solar filter (Gauslaa and Solhaug, 2001) that can protect the symbiotic green algae from excess solar radiation (Nybakken and Gauslaa, 2007). It is thus probable that transplants of *E. mesomorpha* have been affected by other factors than light increases alone, such as an increase in temperature and/or a decrease in water content. By contrast, in our study, the color of many transplants of *B. nadvornikiana* located in partial cuts changed from grey pale to dark brown during the experiment. The dark pigmentation may have served to protect the photobiont against high

light, which may represent a cost for the species and may have diminished growth rates in the short term (Hedenås and Ericsson, 2003).

Increase of temperature with canopy openness – Microclimate data from the partial cuttings and control plots indicates that both air temperature and lichen temperatures were, for both species, higher in partial cuts (compared to control plots). Although increases in thallus temperatures can be positive for net assimilation by canopy lichens, this depends on the trade-off between increases in photosynthesis with increasing temperature, and elevated rates of respiration, which can significantly exceed greater carbon gain from photosynthesis (Palmqvist, 2000). Elevated canopy temperatures can also have a negative impact on lichen survival if growth rates exceed thermal tolerance limits (Kershaw, 1985; Palmqvist and Sundberg, 2000). Some species are particularly heat sensitive. For example, *Lobaria pulmonaria* is highly heat sensitive when the air is dry, being affected already at 40°C (Gauslaa and Solhaug, 1999). According to Nash (1996), net photosynthesis in species from sheltered habitats can decline if temperature is slightly higher than those experienced in their natural microhabitats (Nash, 1996). It is possible that such a decline may have happened in our transplants of *B. nadvornikiana* in partial cuttings. The increase in dark pigmentation observed in our samples after exposure to high irradiance also has the disadvantage of potentially increasing heat loading by increasing absorbance of solar energy (Gauslaa and Solhaug, 2001).

Equally important may be changes in the duration of thallus hydration imposed by higher temperatures in partial cuts. The pendulous thalli of alectorioid lichens have limited water storage capabilities and hence respond quickly to changes in water vapor deficit (Jonsson et.al. 2008). Even small increases in temperature during or after wetting events can lead to dramatically shorter duration of periods of thallus hydration, and thus reduce net assimilation during each wetting-drying cycle (Coxson and Coyle 2003).

Increase of thallus fragmentation with canopy openness – Conditions that give lichens increased exposure to radiation may also result in increases in physical damage (Esseen and

Renhorn, 1998). For instance, greater wind penetration when canopy gaps are created rapidly can lead to fragmentation of epiphytic lichens and could restrain biomass accumulation. For example, growth rate of *Alectoria sarmentosa* decreases from 11.5% to 7% when thallus fragmentation is considered (Renhorn and Esseen, 1995). As pointed out by Gauslaa *et al.* (2007), environmental conditions allowing for higher growth rates may be a prerequisite to balance the heavy loss of detached thalli that occurs in dynamic tree canopies.

In our study, we did not quantify the fragmentation rate, but in general we observed few fragments of *E. mesomorpha* in the bottom of the cages, whereas *B. nadvornikiana* lost many fragments. Liberation and transport of thallus fragments is a known dispersal strategy for *Bryoria* (Esseen, 1985; Stevenson, 1988; Dettki, 1998), whereas dispersal is mainly insured by soredia in *E. mesomorpha* (Brodo *et al.*, 2001). Thallus fragmentation did not seem to be an important factor to explain the decrease of *E. mesomorpha* growth in partial cuts. However, indirect evidence indicates that this phenomenon might be important to explain the low *B. nadvornikiana* growth in partial cuts compared with control plots. Indeed, because the mean difference between photosynthetic and respiratory rates between controls and partial cuts are small (not significant), the negative growth response to partial harvestings could be mainly a fragmentation response.

4.7 Conclusion

Overall, despite the relatively high variability in the observed growth rates in the two treatments, the results of this study suggest that canopy openings have a relatively negative effect on lichen growth for the studied species (*B. nadvornikiana* and *E. mesomorpha*). When all environmental factors are considered, the most important appears to have been a reduced period of metabolic activity, resulting from drier conditions in the partial cut treatments, particularly during the second year, which was exceptionally dry. Lichen growth rate seems to be influenced at the same time by factors acting at the scale of individual thalli, such as light levels above each cage (canopy openness), and factors operating at the scale of the plot,

such as basal area and stem density. These plot-level factors can have a major impact on air humidity, air temperature, and wind penetration, all of which can limit periods of hydration in lichen thalli. On average, partial cuts in this experiment may not provide enough residual trees to buffer the effects of an increased exposure, such as greater insolation, more wind exposure, and lower humidity (Stevenson and Coxson, 2007).

At the landscape scale, our results suggest that if the remaining old forests patches are systematically treated with partial cuts of the kind that were studied, there is a risk that lichen growth will be negatively affected, both at the individual and at the population level. Inferior growth rates in partial cutting treatments might indicate that health status of the population is declining, and suggest that some processes such as lichen reproduction (Gauslaa *et al.*, 2007) may also be negatively affected, at least during the acclimation period following the cuts. Because this negative effect could be more likely to occur during relatively dry years, as was observed in this study, future trends in the response of epiphytic lichens to the creation of canopy openings could be influenced by climate change (Bergeron *et al.*, 2010).

Even if partially harvested stands are not an equivalent habitat compared with old-growth forests, partial harvests remain an interesting silvicultural alternative to clearcutting in order to maintain minimal epiphytic lichen populations in a given location. It is important to emphasize that even if the mean growth response is negative following partial cuts, there is a high variability and growth reductions are much less pronounced when residual canopy is relatively dense (see fig. 4.6 a and 4.b). The residual trees may function as important refugia from which future lichen propagules can disperse to regenerating trees (Peck and McCune, 1997; Hazell and Gustafsson, 1999; Lõhmus *et al.*, 2006), especially if these residual trees are large and/or old (Esseen *et al.*, 1996; Boudreault *et al.*, 2009). In order to minimize the impact of partial cuttings on species associated with overmature and old-growth forests, forest harvestings that maintain a relatively closed-canopy cover, or that maintain intact clumps of residual tree within the treated stands (Hazell and Gustafsson, 1999), should be prioritized over uniform partial cuttings with high levels of tree removal. Partially harvested

stands could still be useful in this context to buffer edge effects around patches of untreated forests (Coxson and Stevenson, 2008; Stevenson and Coxson, 2007b).

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4.9 Tables

Table 4.1 Mean ± SD of canopy openness, stem density, and basal area for each treatment and site and for all sites combined

	Canopy openness (%) (n = 12)	Stem density (no./ha) (n =12)	Basal area (m^2/ha) (n = 12)
Maïcasagi			
Control	19.6 ± 4.3	533.3 ± 212.0	29.7 ± 3.3
Partial cut	39.3 ± 11.3	1357.5 ± 437.6	8.6 ± 1.6
Muskuchii			
Control	14.3 ±2.1	954.2 ± 521.3	27.6 ± 1.7
Partial cut	32.0 ± 10.7	1752.8 ± 480.6	10.1 ± 2.2
Fénélon			
Control	24.0 ± 7.5	535.4 ± 337.9	28.1 ± 2.6
Partial cut	51.0 ± 15.3	1275.0 ± 295.6	8.1 ± 2.3
All sites combined			
Control	19.6 ± 6.6	674.3 ± 419.2	28.5 ± 1.5
Partial cut	41.1 ± 15.0	1440.3 ± 440.0	8.9 ± 1.2

Table 4.2 Repeated measure analyses of variance comparing biomass of *Bryoria nadvornnikiana* and *Evernia mesomorpha* between treatments and seasons

		df	*F*	*p*
Bryoria nadvornikiana				
Between-subject effect				
	Treatment	1, 66.6	19.63	**<0.001**
Within-subject effects				
	Season	3, 478	3.19	**0.024**
	Treatment x season	3, 439	26.77	**<0.001**
	Number of days within season	1, 452	3, 61	0.058
Evernia mesomorpha				
Between-subject effect				
	Treatment	1, 71.8	4.88	**0.030**
Within-subject effects				
	Season	3, 410	0.36	0.781
	Treatment x season	3, 370	8.73	**<0.001**
	Number of days within season	1, 383	0.22	0.637

Note: Significant values ($p \leq 0.05$) are given in boldface. Site and sampling plot nested within the site were random factors. The random effects were used as error term when testing for differences between fixed effects.

Table 4.3 Mean rates of net photosynthesis and dark respiration for *Bryoria nadvornikiana* and *Evernia mesomorpha* in control and partial-cut plots, measured at the end of the experiment

	Control		Partial cut			
	Mean	SD	Mean	SD	*F*	*p*
Bryoria nadvornikiana						
Net photosynthesis	0.704	0.430	0.620	0.684	2.58	0.111
Dark respiration	-0.456	0.279	-0.450	0.188	0.02	0.901
Evernia mesomorpha						
Net photosynthesis	0.628	0.390	0.512	0.367	2.55	0.113
Dark respiration	-0.359	0.205	-0.370	0.165	0.09	0.771

Note. One-way ANOVAs were used to compare net photosynthesis and dark respiration. $n = 67$ and 55 for *Bryoria nadvornikiana* in control and partial cut, respectively; $n = 55$ for *Evenia mesomorph*a in control and partial cut.

4.10 Figures

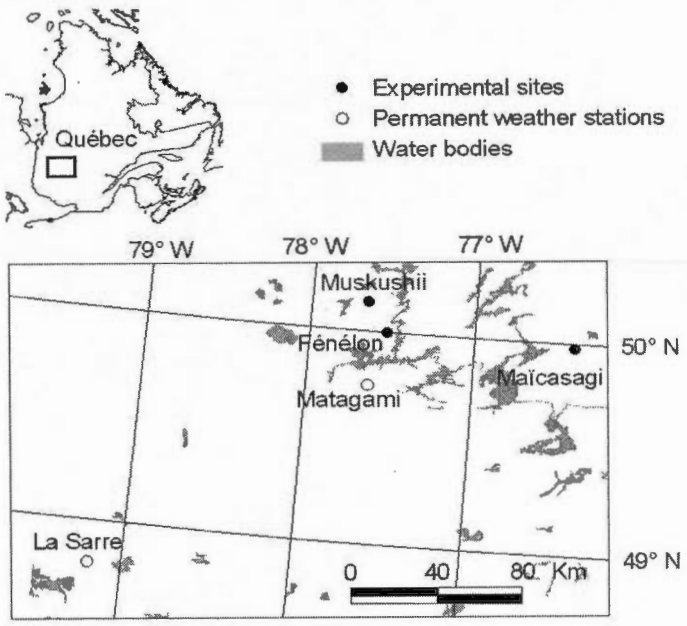

Figure 4.1 Map of the study area.

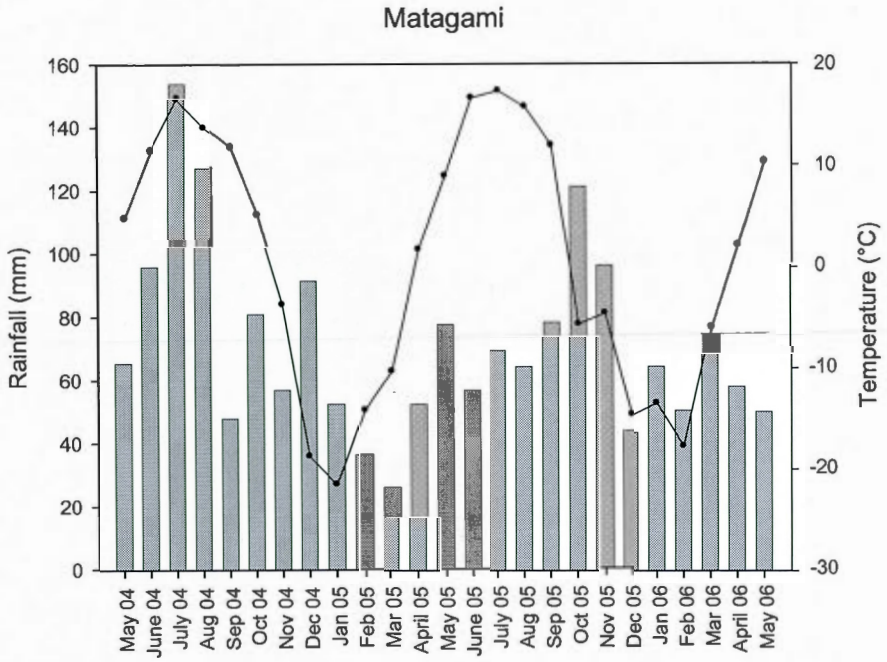

Figure 4.2 Monthly rainfall and temperature (mean) recorded at the Matagami weather station during the study. Bars represent rainfall and line represents temperature.

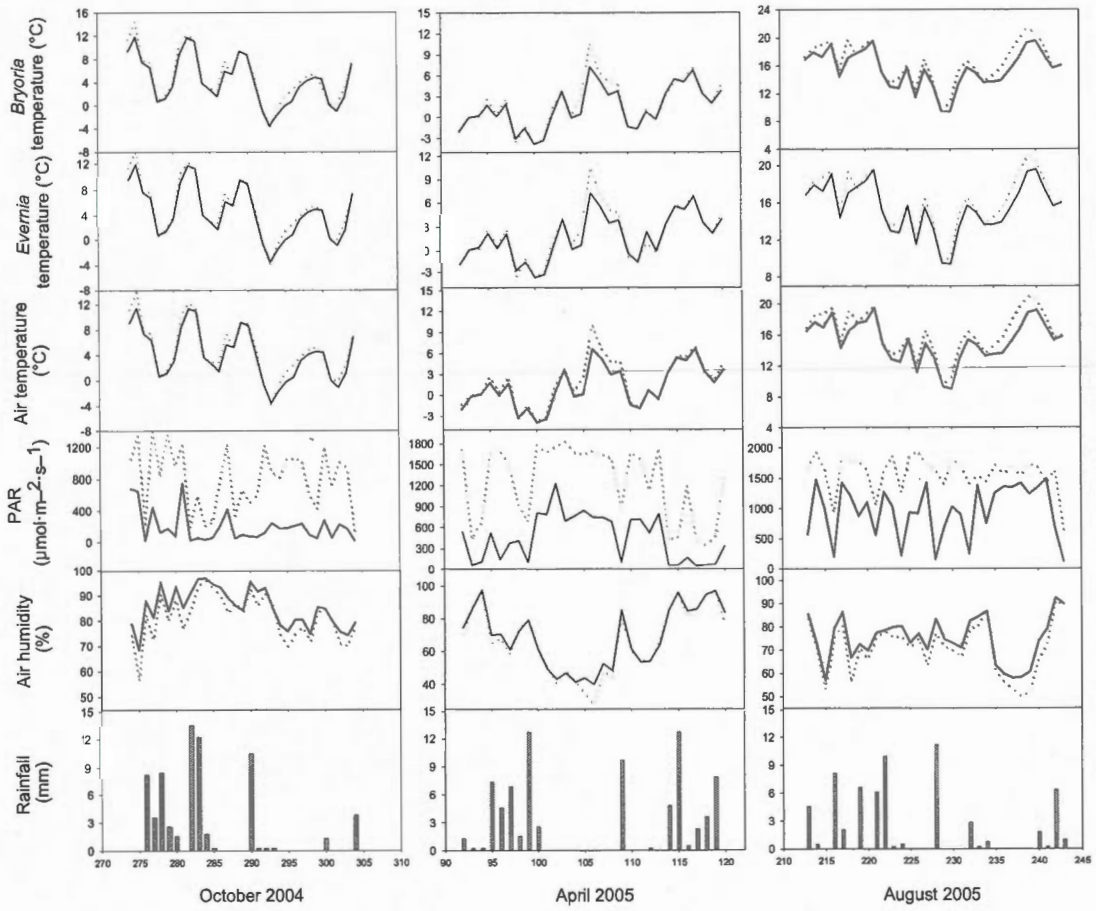

Figure 4.3 Summary of microclimate data for October 2004, April 2005, and July 2005 at Maïcasagi site. The lines for *Bryoria* temperature, *Evernia* temperature, and photosynthetically active radiation (PAR) are the average of all sensors within a plot. Solid lines are for control plots and dashed lines are for partial cuts. The x-axis represents day numbers.

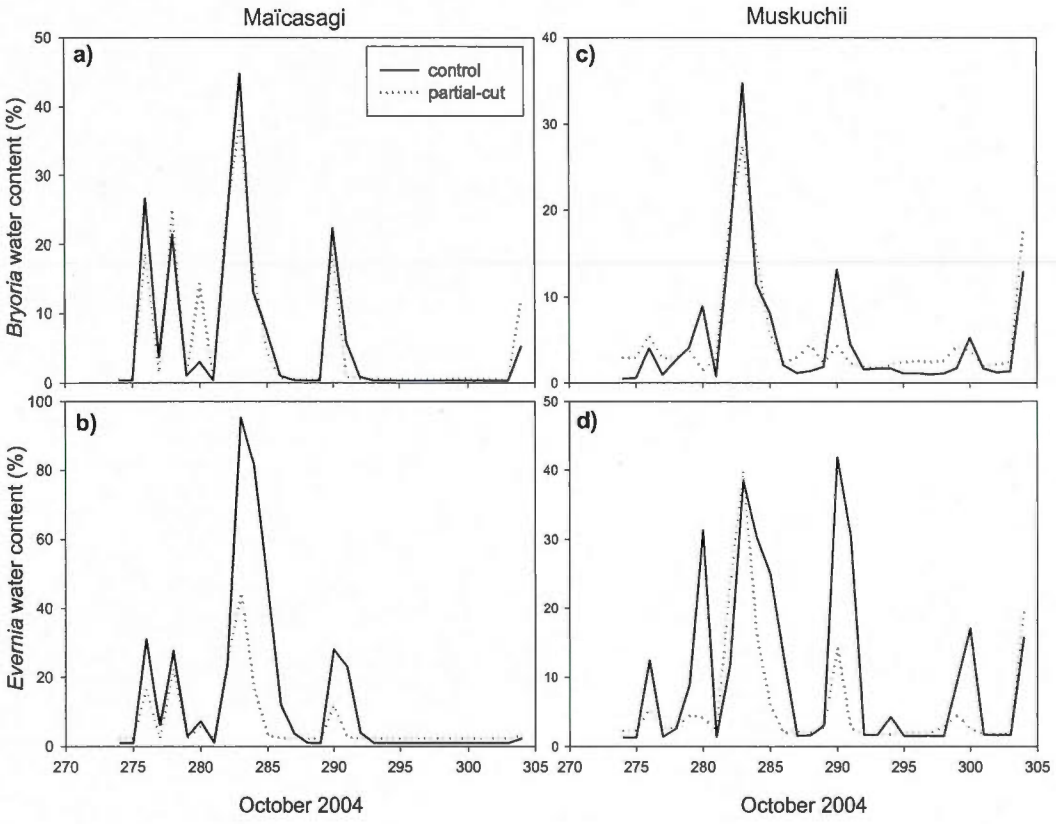

Figure 4.4 Summary of thalli water content for October 2004 at Maïcasagi site (a and b) and Muskuchii site (c and d). The lines are the average of all sensors within a plot. Solid lines are for control plots and dashed lines are for partial cuts. The x-axis represents day numbers.

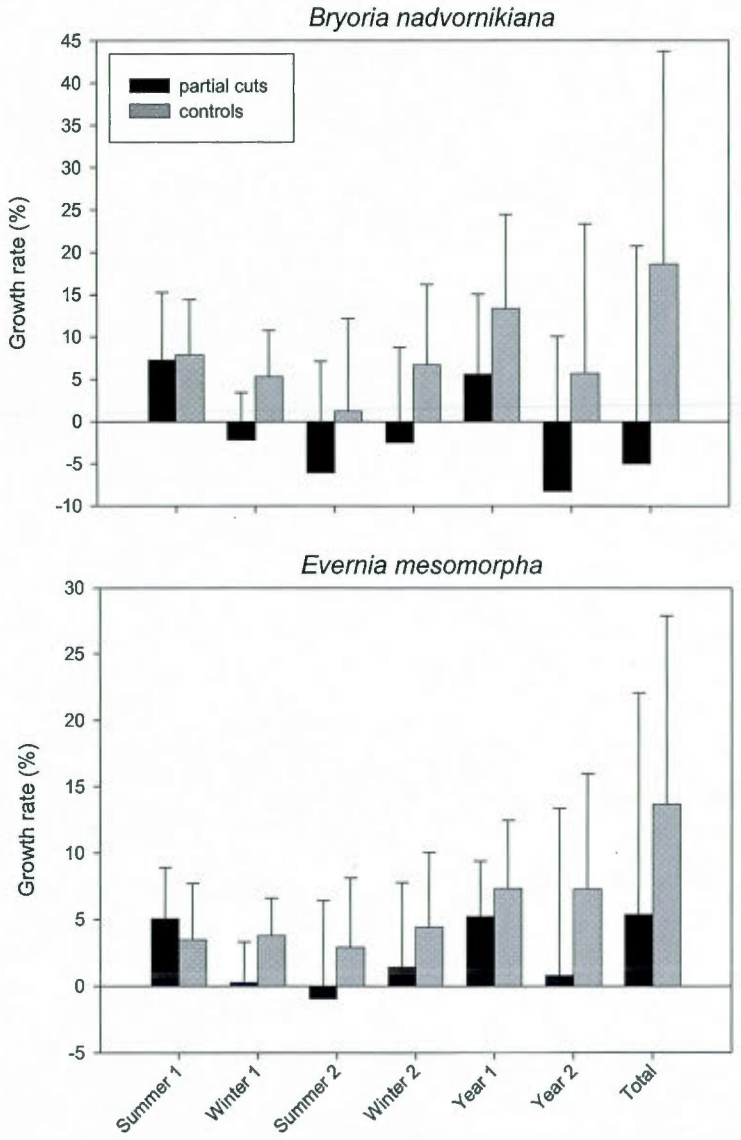

Figure 4.5 Growth rates of *Bryoria nadvornikiana* and *Evernia mesomorpha* by treatment for each season, at the end of each year, and at the end of the experiment. Bars are means of growth rate. Error bars are SDs.

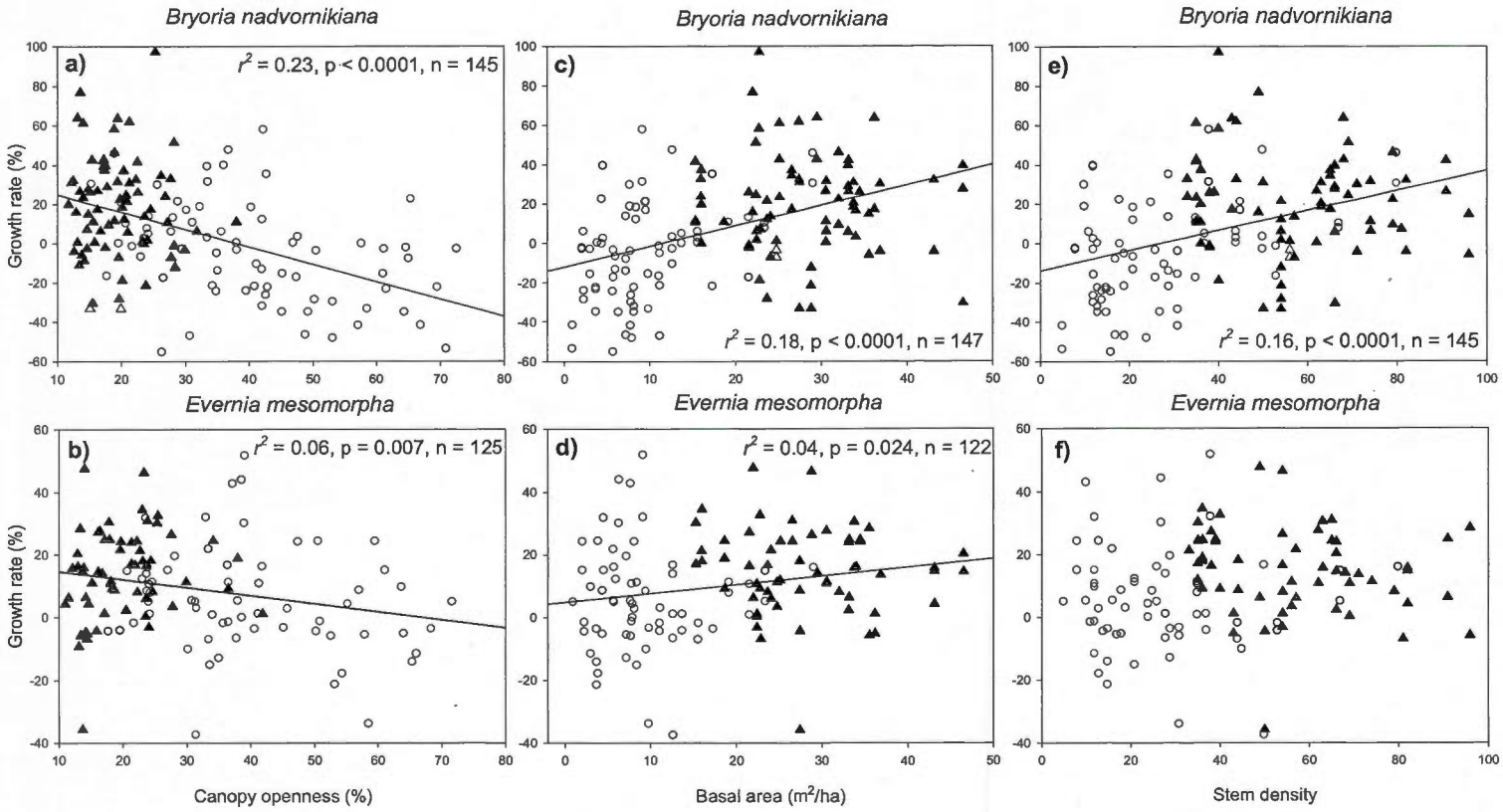

Figure 4.6 Linear regressions between total growth of each species at the end of the experiment and canopy openness as measured by hemispherical photographs (a and b), basal area (c and d), and stem density (e and f). Lines are shown only for significant relationships. Empty circles are for lichen from partial cuts and solid triangles are for lichens from control plots.

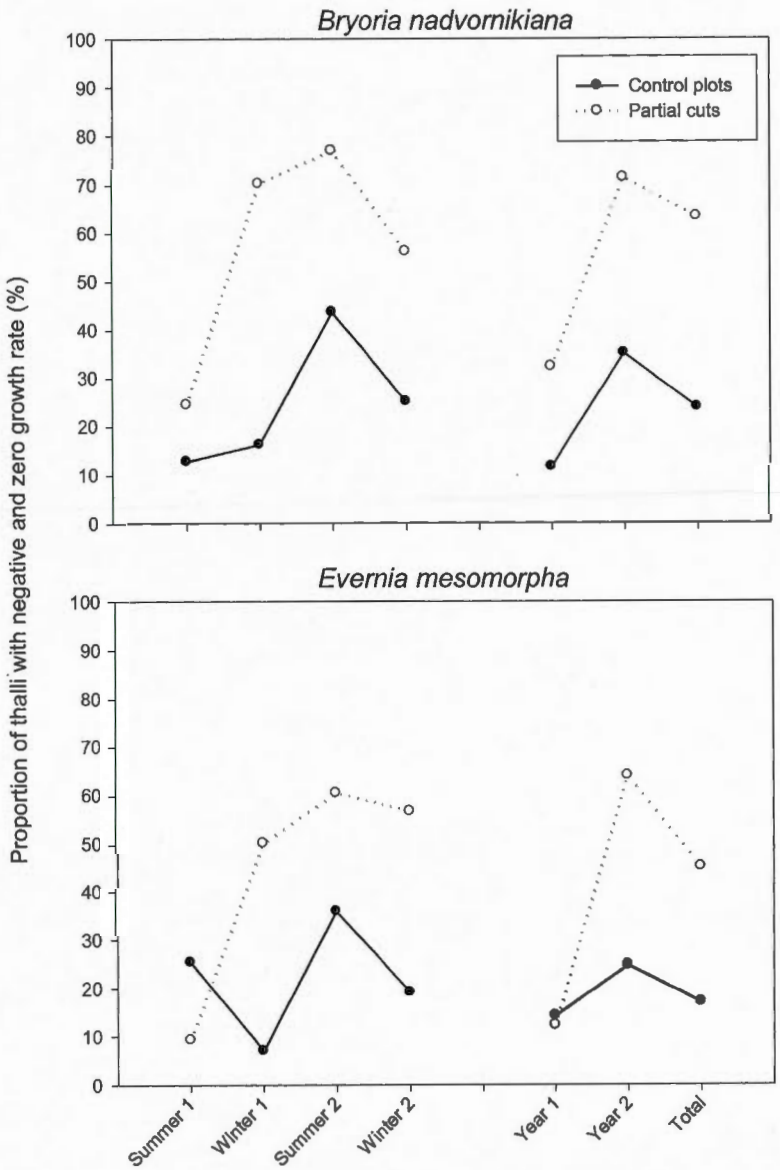

Figure 4.7 Proportion of thalli with negative or zero growth rates in both treatments for each season, at the end of each year, and at the end of the experiment.

CONCLUSION GÉNÉRALE

Cette thèse apporte des connaissances fondamentales sur les populations de lichens épiphytes dans les pessières à mousses de l'Ouest du Québec. Peu d'études ont été consacrées à ce jour à ces organismes pourtant importants dans cet écosystème, tant au niveau de la richesse que de l'abondance (Boudreault *et al.*, 2002; Yarranton, 1972). De plus, dans un contexte d'aménagement écosystémique qui vise à aménager de façon durable les forêts, cette thèse nous fournit des indications quant aux impacts que peuvent avoir les coupes totales et les coupes partielles pour des organismes qui dépendent des conditions forestières d'intérieur. Enfin, elle nous permet de cibler des éléments de structure des forêts qu'il faut conserver ou recréer pour maximiser les chances de maintenir la diversité biologique des lichens épiphytes, tant à l'échelle locale du peuplement qu'à l'échelle du paysage. Dans cette section, je ferai d'abord un résumé des connaissances acquises dans cette étude qui nous permettent d'évaluer quelles sont les conditions forestières importantes pour les lichens épiphytes et quels sont les impacts de la fragmentation sur ces organismes. À travers ce résumé, je ferai également ressortir les points importants pouvant servir à adapter l'aménagement forestier afin de respecter les objectifs de maintien de la diversité. Enfin, je discuterai de certaines limites de mon étude et formulerai des idées concernant de futures études sur les lichens épiphytes qui pourraient être entreprises.

5.1. Conditions forestières favorisant l'accumulation des lichens épiphytes dans la pessière à mousses de l'Abitibi

Les résultats des quatre chapitres montrent que l'accumulation de biomasse en lichens épiphytes dans les forêts est un processus complexe, dépendant de plusieurs facteurs biotiques et abiotiques, affectant directement (p. ex., croissance, fragmentation des thalles) ou indirectement (p. ex., diminution de la quantité de substrats) les lichens épiphytes.

Les données de biomasse nous indiquent que les espèces du groupe *Bryoria* sont nettement dominantes parmi les lichens fruticuleux dans la canopée des arbres des forêts matures et anciennes, à la fois dans la portion Ouest (chapitre 1) et la portion Est (chapitre 2) de l'Abitibi. Dans la portion Est, l'abondance des lichens fruticuleux est supérieure à celle des lichens foliacés (chapitre 3), de même que dans la portion Ouest de l'Abitibi (C. Boudreault, résultats non publiés). Cette dominance des lichens fruticuleux sur les lichens foliacés dans les forêts non aménagées au niveau de l'abondance a été également observée en Suède (Dettki et Esseen, 1998; Esseen *et al.*, 1996). Dans les forêts pluvieuses de la côte du Pacifique cependant, les cyanolichens sont beaucoup plus abondants que les lichens fruticuleux (McCune, 1993). Au niveau des jeunes forêts en régénération, les lichens foliacés sont dominants, à la fois dans les peuplements régénérés naturellement et dans les plantations, et à la fois au niveau du nombre de thalles établis et du recouvrement (chapitre 3).

Certaines espèces typiquement associées aux forêts boréales telles que *Platismatia glauca*, *Lobaria pulmonaria*, *Alectoria sarmentosa* et *Usnea longissima*, bien que présentes sur le territoire, sont souvent restreintes à des habitats particulièrement humides (C. Boudreault, observation personnelle). Le climat continental plus sec comparativement au climat semi-maritime observé dans l'Est du Québec et en Fennoscandinavie (Kneeshaw *et al.*, sous presse) pourrait expliquer la rareté de ces espèces dans la région étudiée.

Les résultats obtenus dans les trois premiers chapitres montrent que la biomasse des lichens varie en fonction de la qualité et de la quantité des substrats disponibles pour la colonisation, tant à l'échelle de la branche, de l'arbre et du peuplement. À l'échelle de la branche, les résultats obtenus dans les chapitres 1, 2 et 3 montrent que la biomasse en lichens épiphytes augmente en fonction de la longueur de la branche (chapitres 1, 2 et 3) et de son diamètre (chapitres 2 et 3), que les branches vivantes sont de meilleurs substrats que les branches mortes (chapitres 1 et 2) et que le nombre et l'abondance des lichens augmentent en fonction de l'âge du substrat (chapitre 3).

À l'échelle de l'arbre, les arbres de plus gros diamètres (> 16 cm), plus hauts, avec plus de branches et des branches plus longues comportaient une plus forte biomasse de lichens des trois genres étudiés (*Bryoria*, *Evernia* et *Usnea*) que les arbres plus petits (< 16 cm). La biomasse était maximale sur les arbres d'environ 150 ans. La biomasse déclinait par la suite sur les arbres plus vieux vraisemblablement en raison d'une diminution du nombre de branches par arbre en fonction de l'âge des arbres. Les résultats obtenus dans le chapitre 3 montrent également que le nombre de thalles et l'abondance des lichens sur les branches prélevées dans les plantations augmentent avec la taille des arbres, probablement en raison d'une relation positive entre le diamètre et l'âge des arbres. Une plus forte biomasse de lichens a aussi été observée dans la strate intermédiaire des arbres (entre 5 et 10 m de hauteur; chapitre 1), où les branches étaient plus longues et plus nombreuses. Ces résultats corroborent ceux généralement observés dans la littérature (Arseneau *et al.*, 1997; Lang *et al.*, 1980; Lui *et al.*, 2000). Cependant, aucun changement de composition en espèces en fonction de la hauteur des branches (zonation verticale) n'a été remarqué, ce qui contraste avec les résultats présentés dans plusieurs autres études (Campbell et Coxson, 2001; McCune, 1993). Notons que les arbres étudiés, avec une taille moyenne de ~13,5 m (comparativement à des arbres pouvant atteindre plus de 65 m sur la côte du Pacifique [McCune, 1993]), n'étaient probablement pas assez hauts pour que les différences de conditions environnementales entre les classes de hauteur soient assez prononcées pour créer des niches écologiques distinctes.

Le chapitre 1 a montré que l'abondance des *Bryoria* et des *Usnea* dans les forêts naturelles variait en fonction du temps écoulé depuis le dernier feu, pour atteindre une biomasse maximale dans les peuplements surannés (101-200 ans), et ensuite décliner dans les peuplements plus anciens (> 200 ans). La biomasse d'*Evernia mesomorpha* était plus stable dans le temps et déclinait dans les plus vieux peuplements (> 200 ans), mais seulement lorsque la biomasse était estimée à l'échelle du peuplement. Dans le cas particulier de la pessière à mousses de l'Abitibi, le déclin observé dans les plus vieux peuplements (> 200 ans; chapitre 1) chez les trois groupes de lichens étudiés peut être en partie expliqué par la plus faible densité de tiges qui prévaut dans ces vieux peuplements paludifiés. Comme l'ont

montré d'autres études (Lesica *et al.*, 1991; Neitlich, 1993; Esseen *et al.*, 1996), les jeunes peuplements (50-100 ans) avaient une faible biomasse en lichens épiphytes comparativement aux autres stades successionnels (p. ex., près de 4 fois moins de *Bryoria* que dans les forêts âgées de 101-150 ans). Dans ces jeunes peuplements, il n'y avait pas moins de gros arbres (> 16 cm), les arbres n'y étaient pas moins hauts, mais la structure du peuplement était toutefois différente (plus forte densité de tiges et plus forte surface terrière) et les peuplements présentaient peu d'ouvertures (St-Denis *et al.*, 2010). De plus, les arbres des jeunes peuplements étaient en moyenne deux fois plus jeunes que ceux du stade de développement suivant (100-150 ans).

La biomasse des lichens épiphytes s'accumule donc lentement dans les forêts et, par conséquent, une révolution forestière de 100 ans, éliminant les forêts les plus productives (101-200 ans) et conservant uniquement les forêts les plus vieilles et moins productives ainsi que les jeunes peuplements, ne permettra pas de maintenir les populations de lichens épiphytes à un niveau comparable à ce qui pourrait être observé dans un paysage naturel. Mon étude ne permet pas d'évaluer directement si les lichens épiphytes fruticuleux s'accumulent lentement dans les forêts en raison de limitation dans leur capacité de dispersion. Les résultats présentés au chapitre 3 montrent néanmoins que les espèces communes sont capables de se disperser sur des distances de 100 m. Il est vraisemblable que les lichens fruticuleux verront leur chance d'atteindre un site et de le coloniser augmenter en fonction du temps écoulé depuis la perturbation, dans la mesure où des substrats adéquats sont disponibles. D'ailleurs, les résultats du chapitre 3 montrent que les lichens fruticuleux étaient très peu représentés dans les aires en régénération et que leur abondance était très faible comparativement aux forêts adjacentes non coupées. De plus, comme le suggère Sillett *et al.* (2000) pour expliquer le faible taux d'établissement et la faible abondance des lichens alectorioides dans les jeunes forêts fermées, la structure des forêts qui change en fonction du temps écoulé depuis la perturbation serait plus importante pour expliquer l'association de ce groupe d'espèces avec les vieilles forêts que des limitations dans leur capacité de dispersion.

La structure du couvert forestier influence fortement les conditions environnementales prévalant dans les forêts et ces conditions auront une influence importante sur les divers processus permettant aux populations de lichens épiphytes de se maintenir dans les paysages naturels ou aménagés. L'ouverture de la canopée avec le temps depuis le dernier feu (~100 ans) favorise la pénétration de la lumière et de l'humidité (Geiger, 1965, McCune, 1993) et l'accumulation de lichens épiphytes dans les forêts. Par exemple, plusieurs études montrent que la croissance des lichens est limitée dans les forêts fermées en raison de la faible luminosité et qu'une ouverture du couvert pourrait favoriser la croissance (Gauslaa *et al.*, 2006; Gauslaa *et al.*, 2007; Jansson *et al.*, 2009). Toutefois, les résultats du chapitre 4 tendent à montrer que l'ouverture du couvert forestier par des coupes partielles, lorsque le prélèvement est trop important, ne permet pas de maintenir les conditions forestières appropriées pour permettre l'accroissement en biomasse des deux espèces étudiées. Mes résultats suggèrent que des modifications au niveau des conditions d'humidité dans les coupes partielles dues à l'effet combiné d'une augmentation de la lumière, de la température et d'une plus grande pénétration par le vent ont eu pour conséquence de réduire la durée de la période d'hydratation des transplants. C'est durant cette période que la photosynthèse peut se réaliser et mener à un accroissement de la biomasse des lichens. Les résultats semblent montrer que les effets des coupes partielles sur la croissance des lichens pourraient être exacerbés lors des saisons particulièrement sèches (p. ex., deuxième année de l'étude) et dans des régions particulièrement sèches comme celle étudiée. Je suggère également que la plus faible biomasse observée à l'échelle de la branche et de l'arbre (*Bryoria* et *Usnea*) dans les forêts de plus de 200 ans caractérisées par la présence de grandes trouées (St-Denis et *al.*, 2010; chapitre 1) pourrait être en partie expliquée par une réduction de la durée des périodes d'hydratation ainsi que par une augmentation de la fragmentation des thalles.

Les résultats obtenus dans les chapitres 1, 2 et 4 supportent l'hypothèse que la pénétration du vent dans les forêts lorsque le couvert forestier est ouvert peut avoir un effet significatif sur la fragmentation des thalles, particulièrement pour les *Bryoria*. Ce phénomène, bien que naturel et permettant aux lichens de se disperser (chapitre 3), serait amplifié par les coupes

forestières et pourrait contribuer à diminuer drastiquement l'accumulation de lichens dans un paysage aménagé par des coupes totales (effets de lisière; chapitre 2) ou par des coupes partielles lorsque la proportion du couvert prélevée est trop importante (chapitre 4).

Les coupes partielles constituent tout de même une alternative intéressante aux coupes totales pour les lichens épiphytes puisqu'elles permettent, contrairement aux coupes totales qui éliminent localement leur habitat, de maintenir une certaine quantité de substrats qui pourront servir à assurer la recolonisation des jeunes arbres avoisinants ou ceux des chantiers de coupes totales en régénération. Les résultats obtenus dans les trois premiers chapitres nous fournissent des indications quant à la qualité des substrats à retenir pour maximiser les chances de préserver les lichens épiphytes des genres *Bryoria*, *Evernia* et *Usnea*. La sélection des arbres devrait d'abord se faire sur leur taille (chapitre 1), soit des arbres > 16 cm. De plus, ces arbres devraient posséder un grand nombre de branches (particulièrement dans la strate de hauteur située entre 5 et 10 m; chapitre 1) et, pour offrir le maximum de microsites permettant aux espèces de s'établir, une forte proportion de ces branches devraient être longues (chapitres 1, 2 et 3) et vivantes (chapitres 1 et 2).

À l'échelle du paysage, les résultats du chapitre 2 montrent que les forêts résiduelles n'ont pas toutes la même valeur pour la conservation des lichens épiphytes fruticuleux. Une plus faible abondance de lichens a été observée dans les séparateurs de coupe comparativement aux grands blocs de forêts résiduelles et aux forêts témoins (chapitre 2). Ces résultats confirment que la qualité des forêts résiduelles pour assurer le maintien des espèces associées aux conditions d'intérieur des forêts dépend fortement de leur taille et de leur forme. De plus, la bordure des ruisseaux (bandes riveraines) semblait constituer un habitat distinct, plus ensoleillé, avec une plus forte présence d'*E. mesomorpha* (chapitre 2). Il est probable que cet habitat particulier abrite aussi un cortège d'espèces de lichens différentes et que leur conservation constitue un enjeu important pour la biodiversité comme l'ont montré plusieurs études réalisées sur d'autres groupes d'organismes (Hylander *et al.* 2005; Naiman *et al.*, 2000).

Une forte proportion du territoire dans un paysage aménagé est occupée par des aires en régénération. Dans le chapitre 2, j'ai comparé la colonisation des lichens épiphytes sur des branches de petits arbres en régénération provenant des deux types de peuplements en régénération observés dans le paysage, soit des peuplements qui se sont régénérés naturellement et des peuplements qui ont été reboisés. Les résultats indiquaient que la colonisation était supérieure dans les peuplements en régénération comparativement aux plantations dans les jeunes coupes (6-10 ans), mais que cette différence s'estompait dans les plus vieilles coupes (12-18 ans). La différence dans les jeunes coupes s'expliquait notamment par la présence de lichens sur la régénération préétablie comparativement aux arbres plantés initialement dépourvus de lichens. Ces résultats indiquent que les plantations, lorsque la régénération préétablie est déficiente, fournissent des substrats intéressants pour la colonisation des lichens épiphytes.

5.2. Impacts de la fragmentation sur les lichens épiphytes

Les résultats présentés dans le chapitre 2 montrent que les habitats linéaires étroits (60 m de largeur) de petite taille conservent peu d'habitats d'intérieur pour les trois groupes d'espèces étudiées (*Bryoria*, *Evernia* et *Usnea*) comparativement aux forêts plus grandes présentant une seule bordure. Même si des effets de lisère ont aussi été observés en bordure de coupes pour les grands blocs de forêts résiduelles (0-15 m) la magnitude de l'effet (biomasse en bordure/biomasse à l'intérieur) était supérieure dans les séparateurs de coupe que dans les grands blocs de forêts résiduelles, ce qui corrobore la théorie que les corridors longs et étroits sont plus affectés par les effets de lisière que les plus grands habitats (Saunders *et al.*, 1991). Les séparateurs de coupe étaient affectés sur au moins 50% de leur largeur par des effets de lisière (chapitre 2). Les résultats suggèrent qu'une diminution de la qualité des branches en bordure (diamètre plus faible) ainsi que des modifications au niveau des conditions environnementales seraient en cause pour expliquer la plus faible biomasse des trois groupes d'espèces observée en bordure des coupes (0-15 m pour *Bryoria* et 0 m pour *Usnea* et *Evernia*). De plus, à l'échelle du peuplement, les arbres renversés en bordure des coupes

constituent une perte nette de substrats pour les lichens épiphytes (Mascarúa López *et al.*, 2006; Rheault *et al.*, 2003).

Dans le chapitre 3, les forêts sources adjacentes aux coupes, situées dans la même région et semblables à celles étudiées dans le chapitre 2, étaient probablement soumises elles aussi à des effets de lisière. Même si ces effets ont probablement eu pour effet de diminuer en bordure la quantité de propagules disponibles pour assurer la recolonisation des aires de coupe, nos résultats montrent que la plupart des espèces étaient capables de se disperser sur 100 m. Cependant, la faible quantité de thalles retrouvée sur les branches prélevées dans les aires en régénération suggère que 15-20 ans après coupe, les arbres dépendent encore de sources de propagules provenant de forêts matures ou anciennes situées à proximité pour assurer leur colonisation. Cet aspect pourrait être particulièrement important pour assurer la recolonisation des arbres plantés initialement dépourvus de lichens. Dans le contexte actuel, ces forêts sources pourront prochainement être coupées puisque la régénération dans les coupes atteindra bientôt 3 m de hauteur (Gouvernement du Québec, 2011). De plus, des résultats différents auraient pu être observés si les aires de coupe sélectionnées avaient été situées en bordure de séparateurs de coupe plutôt qu'en bordure de grands blocs de forêts résiduelles. Enfin, au moment de l'étude, le paysage forestier entourant les sites étudiés était relativement peu fragmenté. Par conséquent, des effets plus prononcés pourraient être observés à l'avenir à mesure que diminuera la proportion du territoire occupée par des forêts sources et qu'augmenteront les distances entre celles-ci (voir Gu *et al.*, 2001; Fenton et Bergeron 2008; Johansson et Ehrlén, 2003; Öckinger *et al.*, 2004).

Toutefois, je suggère que la fragmentation du paysage aura un effet moins « dévastateur » en forêt boréale continentale canadienne que dans la forêt boréale fennoscandinave. D'abord, bien que des différences fondamentales existent entre les coupes et les feux de forêts, les espèces sont néanmoins adaptées aux feux de couronne plus destructeurs que les feux de surface typiquement observés en Fennoscandinavie (Kneeshaw *et al.*, sous presse). Cette adaptation pourrait constituer un avantage pour permettre aux espèces de persister dans un

paysage aménagé par des coupes forestières. Ensuite, la grande étendue de cet écosystème, le faible niveau d'occupation du territoire et de fragmentation du territoire par le réseau routier par rapport à la forêt boréale fennoscandinave constituent également des avantages. Enfin, dans certaines régions du Québec, l'exploitation relativement récente de nos forêts constitue un avantage puisqu'il est probablement possible de modifier rapidement l'aménagement des forêts avant que les derniers grands massifs de forêts boréales ne soient exploités et fragmentés.

La rétention de groupes d'arbres dans les parterres de coupe totale et l'utilisation de coupes partielles en bordure des coupes totales pourraient être utilisées pour diminuer les effets négatifs associés à la fragmentation, tels que les effets de lisière, les problèmes de recolonisation des aires de coupe et de connectivité entre les habitats résiduels. Les résultats du chapitre 4 indiquent que lorsque l'on utilise des formes de coupes totales avec rétention d'un certain nombre de tiges matures, la rétention de petits groupes d'arbres (« bouquets ») plutôt que d'arbres isolés pourrait limiter les effets néfastes associés à une trop grande ouverture du couvert forestier sur les lichens épiphytes. Puisque les *Bryoria*, le groupe d'espèces qui semble le plus limité dans la dispersion, sont capables de se disperser efficacement sur des distances de 50 m d'un habitat source (chapitre 3), des petits groupes d'arbres séparés par des distances de 50 m pourraient être maintenus afin d'assurer la connectivité entre les habitats. L'utilisation de coupes partielles en bordure des blocs de forêts résiduelles non coupées pourrait également diminuer les effets de lisière en assurant une transition plus graduelle entre les coupes totales et les forêts non coupées.

Les résultats des quatre chapitres font ressortir que la conservation permanente d'habitats de qualité est importante pour le maintien des populations de lichens épiphytes fruticuleux. La priorité devrait être mise sur la préservation de forêts productives âgées de 101 à 200 ans, de plus en plus rares dans le paysage. Ces forêts doivent être de grande taille pour offrir une forte proportion d'habitats d'intérieur permettant aux lichens épiphytes de se maintenir à l'échelle locale et de coloniser de nouveaux sites.

5.3. Limites de l'étude, recommandations méthodologiques et perspectives de recherche

La principale limite de cette étude est de travailler à l'aide de groupes d'espèces plutôt que de travailler à l'échelle de l'espèce (chapitres 1 et 2 et pour les *Bryoria* et *Usnea* dans le chapitre 3). À l'intérieur d'un même groupe, certaines espèces peuvent présenter des différences quant à leurs exigences écologiques ou quant à leur capacité de dispersion. Par exemple, dans une étude réalisée dans les forêts au nord du 52^{e} parallèle (résultats non publiés), j'ai observé que les espèces dont le port est buissonnant (e.g. *B. furcellata*) et produisant des sorédies, colonisent relativement tôt les sites et sont déjà abondantes dans les peuplements en régénération (moins de 50 ans). À l'opposé, les espèces plus filamenteuses (*B. lanestris* et *B. trichodes* ssp. *trichodes*) dont le port est retombant et se dispersant probablement davantage à l'aide de fragments de thalles, mettent plus de temps à coloniser un site et sont plus abondantes dans les peuplements mûrs. Par conséquent, il s'avèrerait intéressant de considérer les espèces de *Bryoria* individuellement pour mieux comprendre la relation entre les stades de développement des peuplements et la présence et l'abondance de ce groupe d'espèces. Une telle approche permettrait également de raffiner les recommandations formulées pour l'aménagement forestier. Toutefois, l'estimation de la biomasse lorsque l'on utilise une approche par espèce est une tâche longue et difficile à accomplir qui mène souvent à une réduction du nombre d'échantillons analysés. Il faut donc trouver d'autres façons d'évaluer l'abondance (recouvrement ou fréquence) lorsqu'une telle approche est utilisée.

Cette étude a été consacrée principalement à l'étude des lichens épiphytes fruticuleux et de certaines espèces communes de lichens foliacés. En forêt boréale, la plus grande diversité en espèces est observée à l'intérieur du groupe formé par les lichens crustacés, et certains groupes de lichens sont probablement beaucoup plus vulnérables aux conditions forestières (p. ex., cyanolichens) ou à la fragmentation du paysage que ne peuvent l'être les lichens fruticuleux. Il reste néanmoins qu'en préservant des habitats permettant de maintenir une forte abondance de lichens épiphytes, on permet probablement aussi de maintenir la majorité des autres espèces boréales présentes dans ces forêts. Il serait intéressant d'acquérir les connaissances fondamentales sur l'écologie des lichens foliacés et crustacés en fonction du

temps écoulé depuis le dernier feu et d'établir ensuite le lien entre la présence et l'abondance de ces espèces avec l'abondance en lichens fruticuleux dans les forêts. Dans la planification initiale de la thèse, je visais à faire une analyse détaillée de la biodiversité présente sur les branches récoltées (chapitre 1) mais, par manque de temps, les espèces n'ont pu être identifiées. Les groupes de lichens fruticuleux (*Bryoria*, *Usnea* et *Evernia*) présentent l'avantage d'être facilement identifiables sur le terrain, contrairement aux lichens crustacés dont la taxonomie est très complexe. Ainsi, on pourrait imaginer que des recommandations claires quant aux arbres porteurs d'une forte biomasse en ces lichens à retenir dans les aires de coupe totale pourraient être formulées aux opérateurs forestiers.

Un suivi à long terme des effets des coupes partielles sur les lichens épiphytes devrait être réalisé. Je propose que des arbres soient sélectionnés, si possible avant la coupe sinon le plus tôt possible après la coupe, et que des branches soient marquées pour étudier l'évolution de la croissance et de la vitalité des lichens. Pour ce faire, des méthodes d'estimation de la biomasse, permettant d'intégrer à la fois les processus de croissance et de fragmentation, seraient appropriées. Pour évaluer la biomasse, différentes méthodes ont déjà été proposées dans la littérature, mais l'utilisation de photos des branches permettrait de diminuer les biais liés à l'estimation visuelle de la biomasse par différents utilisateurs.

Concernant le suivi des conditions microclimatiques présenté au chapitre 4, plusieurs embûches ont été rencontrées lors de cette étude ayant eu pour conséquence de diminuer le nombre de données disponibles pour la comparaison des traitements. Un plus grand nombre de visites dans les sites où les senseurs avaient été installés aurait permis de régler plusieurs de ces problèmes plus rapidement, mais l'éloignement des sites rendait ces visites difficiles. Il serait donc important de tenir compte de cet aspect lors de la planification d'un tel projet.

Il serait très intéressant d'étudier d'autres types de substrats présents dans les forêts de cette région et pouvant abriter un cortège d'espèces différentes. Par exemple, plusieurs espèces du groupe des Caliciales sont associées aux gros chicots (Holien, 1996), les cyanolichens sont surtout observés sur les peupliers faux-tremble dans cette région (C. Boudreault, observation

personnelle) et plusieurs lichens crustacés et lichens fruticuleux (p. ex., *Cladonia*) se retrouvent plus fréquemment sur les débris ligneux au sol (Rheault *et al.*, 2009). Enfin, des études devraient être réalisées dans la pessière à mousses de l'Est (plus humide) afin de comparer la réponse des espèces à divers degrés d'ouverture du peuplement et à la fragmentation du paysage à celle observée dans la pessière à mousses de l'Ouest.

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